

THE
AMERICAN NATURALISTVOL. LXIX *September-October, 1935* No. 724THE ROLES OF UNDEVIATING EVOLUTION AND
TRANSFORMATION IN THE ORIGIN OF MAN¹PROFESSOR WILLIAM K. GREGORY
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IN a meeting of physical anthropologists I need not stop to prove by measurements that the greater anthropoid apes have very long arms and short legs, while mankind as a whole has shorter arms and long legs. Opponents of the view that man has sprung from some early member of the Simiidae have therefore argued that the differences in the intermembral index, in the relative lengths of the thumb and the like, show that we have to do with quite different trends of evolution in apes and men, that man is primarily a creature of the plains, while apes are highly specialized for life in the forest, that thus, through the law of irreversibility of evolution, there is an unbridgeable gap between the two groups.

In several previous papers and books I have considered many of these matters in detail and will therefore refer to them here only in so far as they may illustrate a somewhat different theme. My intention to-day is rather to deal with certain forms or appearances of evolution, which I am calling "Undeviating Evolution" and "Transformation" and which, when considered together, appear to throw light upon the nature and limits of the principle of irreversibility.

"Undeviating evolution," as I am using the term, is intended to imply nothing as to causes, but merely to

¹ Read before the American Association of Physical Anthropologists, April 26, 1935.

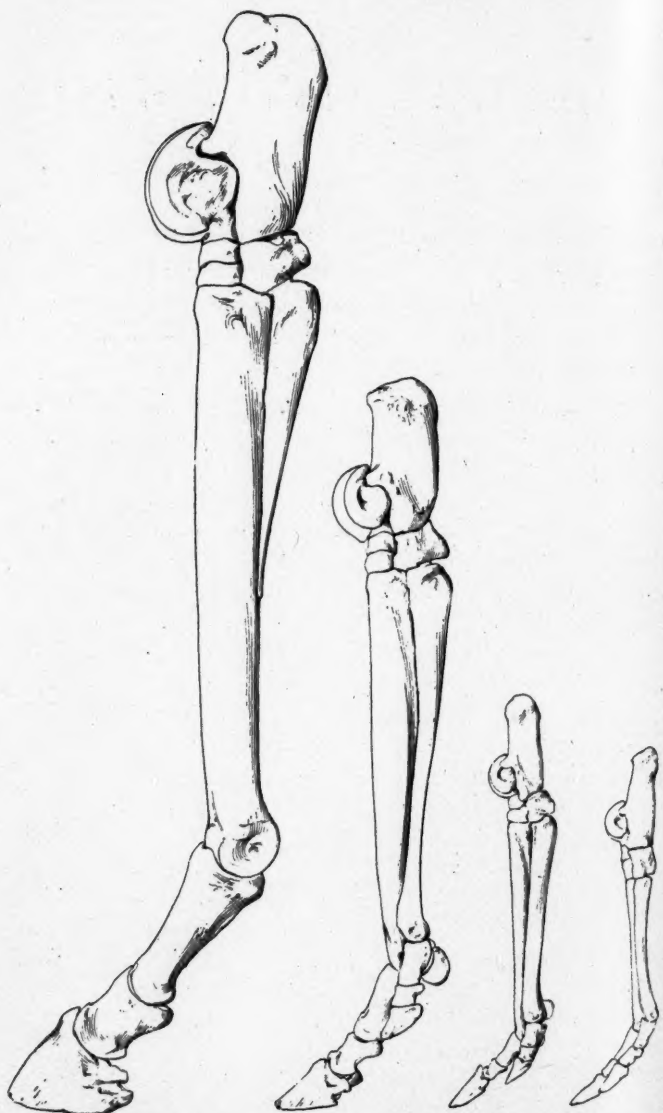


FIG. 1. "Undeviating evolution" of the hind foot of horses from ascending geological levels. (Right to left) 1, *Eohippus*, Eocene Epoch; 2, *Mesohippus*, Oligocene; 3, *Merychippus*, Miocene; 3, *Equus*, Pleistocene and Recent. After W. D. Matthew.

designate cases in which over a fairly long period of geologic time certain characteristics that are already observable in a moderate degree in a remote ancestor become more and more accented in the descendants.

In an evolutionary series of the hind feet of horses from successive geologic horizons, the middle digit, already the largest in the earliest member, becomes more and more dominant, while the lateral digits become relatively smaller, until in the modern horse they are represented merely by vestigial splints at the upper part of the middle metatarsal. Meantime the ungual phalanx of the middle digit has become wider and wider until it dominates the whole lower end of the foot. Thus there is a steady progressive evolution in the same general direction, and the specimens when arranged from left to right according to geologic level strongly suggest one of those double logarithm curves² which are nowadays often in evidence when either ontogenetic or phylogenetic changes conform to the formula $y = ax^k$.

So many examples of this sort of undeviating evolution have been established by the labors of mammalian paleontologists that one might easily get the impression that this is the only way that evolution follows. But the way of evolution that I am here calling "Transformation" is also very evident in many cases.

The typical ichthyosaurs of Lower Jurassic times were so fish-like in general appearance that early paleontologists regarded them as in some way intermediate between fish and reptile. But the discovery of Triassic ichthyosaurs and of the Permian *Mesosaurus* has afforded abundant morphological and paleontological evidence that ichthyosaurs have arisen by transformation from small fluviatile lizard-like reptiles with nearly normal pentadactylate hands and feet. In short, the ordinal habitus of ichthyosaurs is like that of fishes and dolphins, but their class heritage is that of primitive lizard-like reptiles. An evolutionary transformation may therefore

² A. H. Hersh. AMERICAN NATURALIST, 68: November-December, 1934.

be defined as a case in which there has been a profound change both in the life medium and in the anatomical habitus, so that ordinal or family habitus and class heritage are widely different and the descendant bears but little resemblance to its more remote ancestors. Similarly, whales arose by transformation of early terrestrial creodont mammals, bats are transformed arboreal insectivores and birds are "glorified reptiles." In many such cases there is a great mass of morphological and paleontological evidence for the reality of such transformation, evidence which is unfortunately but little known outside the paleontological departments of museums and universities.

It may be advisable, therefore, to give a few moments to the consideration of some remarkable transformations of the locomotor skeleton among the lower vertebrates before endeavoring to apply the principle to the problem of the origin of man.

The researches of Huxley, Dollo, Bensley and later authors on the skull, dentition, feet and other parts of the anatomy of Australian marsupials indicate that the common ancestor of the diprotodont suborder is very



FIG. 2. Ring-tailed phalanger (*Trichosurus*). After J. Bennett. A living fossil, structural ancestor of the kangaroos and *Diprotodon*.

nearly realized in *Trichosurus vulpecula*, the vulpine phalanger, commonly misnamed opossum. This animal is so thoroughly adapted to arboreal life that its hind feet are modified into clamping organs, the enlarged first and fourth digits forming the two arms of the clamp, while the smaller second and third digits are syndactylous, that is, they are closely appressed together, forming a comb for cleaning the fur.

The little musk-kangaroo (*Hypsiprymnodon moschatus*) forms a perfect link between the phalangers and the kangaroos, since its hind foot bears an unmistakable stamp of derivation from the arboreal phalanger type in the enlargement of the fourth digit, in the syndactylous condition of the second and third and in the divergence of the first digit. But "in adaptation" (as the phrase goes) to secondary terrestrial hopping habits, the foot is long and narrow and the first digit much reduced in size. Thus between the phalanger and the musk-kangaroo, with the change from climbing to hopping terrestrial habits, a veritable transformation of the foot has occurred. But from the musk-kangaroo to the common wallabies and kangaroos, evolution is of the undeviating or progressive type, the foot becoming longer, with

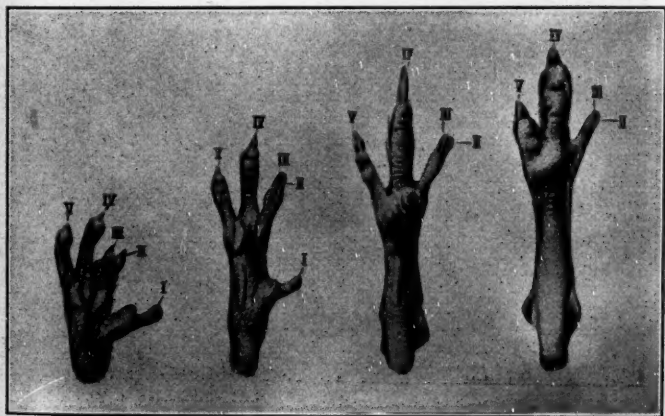


FIG. 3. Hind feet of Australian marsupials. From Gregory, after Bensley.

increasing elongation of the fourth digit and early disappearance of the first. Finally, Dollo and Bensley have shown that in the tree-kangaroo there is a secondary return to life in the trees, accompanied by a new transformation of the foot into a wide cushion, with greatly increased frictional surface of the sole.

Here we have an example of a little-noticed principle which I have observed to be operating in the evolution of many parts of the skeleton of fossil and recent fishes, amphibians, reptiles, birds, mammals. This principle is that any index of length to breadth represents a rectangular figure whose length and breadth, respectively, are the sums of increments that have been added at different periods of evolution. Consequently, identical rectangles may be and are often produced, by convergence, from different factors.

A very surprising but equally well-documented transformation took place when some early race of phalangers climbed down on to the ground and there gave rise to the swarming lines of giant herbivorous marsupials

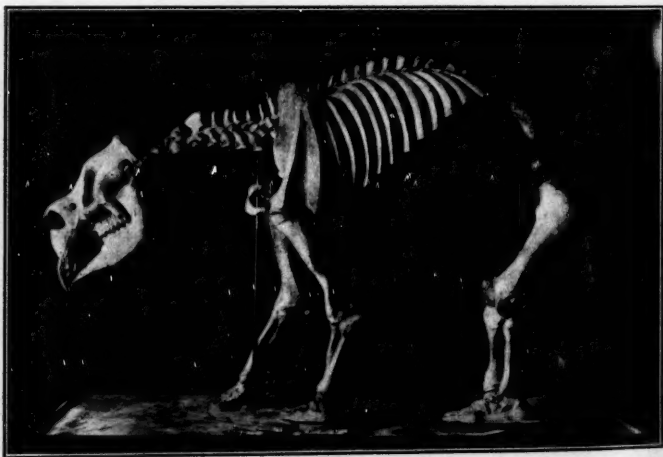


FIG. 4. Cast of skeleton of *Diprotodon*. Mounted in American Museum of Natural History.

known as *Diprotodon*, *Nototherium*, *Euryzygoma*, etc., the fossil remains of which are so abundant in the Pleistocene cave and lake deposits of Australia and Tasmania. The hind foot of these diprotodons, somewhat like that of the ground sloths, is club-footed, with sharply inturned digits and hypertrophied outer border. One dominant

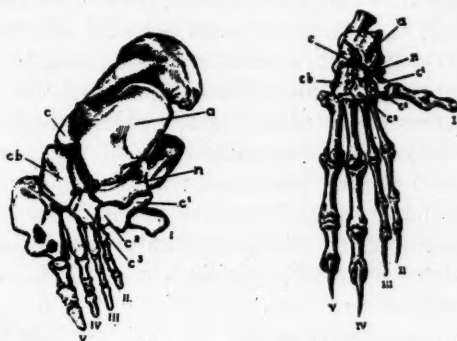


FIG. 5. Hind foot of *Diprotodon* and phalanger (*Trichosurus*). After Dollo.

feature has been the development of a ball-and-socket joint between the lower side of the astragalus and the bones that support it, namely, the calcaneum, the cuboid and navicular, which are arranged as a sort of amphitheater around the astragalus. The metatarsal of the fifth digit is greatly widened. The first digit is represented by a medially directed stump.

The brilliant Dollo saw that this strange type of foot bore many unmistakable traces of derivation from the grasping syndactylous foot of the phalangers and that irreversibility of evolution was illustrated in the retention of a basic pattern disguised by subsequent changes in proportion both of the foot as a whole and of its several parts. Dollo did not, however, call attention to the fact that in this, as in many other instances, the appearance of transformation is produced through excessive emphasis of the transverse diameters of certain parts, following an earlier period of lengthening.

Nor has the principle of irreversibility prevented the digits, which had formerly been lengthening, from later becoming much shortened. Here, then, we have another example of the fact that the indices of length to breadth of individual parts are summations of increments that took place at different periods. Likewise in the case of intermembral ratios in which the length of one part is compared with the length of another, the several lengths represent increments of different age, and to my mind it is incorrect and misleading to regard the total size of the differences between such ratios as being even a rough measure of the magnitude of the phylogenetic gap between the animals measured.

One of the greatest transformations in the locomotor system began when certain air-breathing fishes used their stout pectoral and pelvic paddles to assist the axial mus-

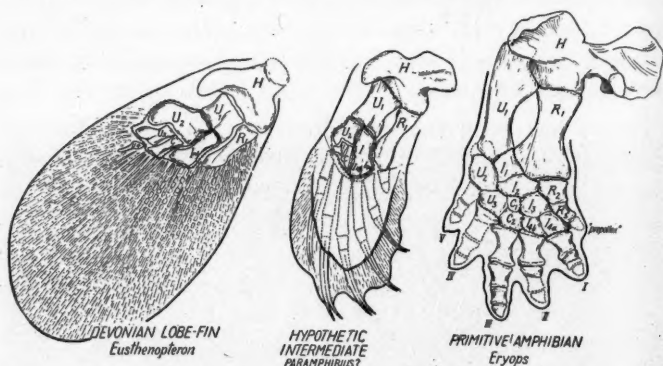


FIG. 6. Transformation of the paddle of *Eusthenopteron* into the five-rayed hand of *Eryops*.

culture and skeleton in pushing the body along on the ground. There is a great morphological gap, however, between the paddle of the Devonian crossopterygian and the five-rayed cheiropterygium of the Carboniferous stegocephalians. Unfortunately, the intermediate stage in the limbs which ought to correspond to the skulls of the recently discovered Upper Devonian stegocephs is

not yet known. The problem at present is how to account for the fact that in the Paleozoic Amphibia all five digits and the numerous carpals converge toward the ulna, or in the pelvic limb, toward the fibula. In 1915 I showed that this convergence of the elements was foreshadowed in the pectoral paddle of the Upper Devonian genera *Eusthenopteron* and *Sauripterus*, and a recent restudy of the material leads to the suggestion that the primitive crossopterygian paddle contains representatives of what may be called the radial, intermedial, central and ulnar parts of the carpus of amphibians. The breaking-up of certain of the rods into the numerous pieces of the stegoccephalian carpus may be supposed to have been initiated in embryonic stages, perhaps in connection with changing positions and subdivisions of the fan-like extensor, flexor, pronator and supinator muscles of the primitive forearm and hand, the joints in the carpus of amphibians being at right angles to the direction of pull of the muscles.³

In later vertebrates, with the drawing in of the feet toward the midline there was a realignment of the carpals and tarsals so that they came to be arranged in transverse rather than oblique rows.

In the most primitive known placental mammals, which are certain of the creodonts of the Lower Eocene, the pentadactylate hands and feet have evenly diverging digits, with no special emphasis of the thumb or of the great toe. In the oldest known Primates, however, the great toe is already much stouter than any of the others and it is set off at a sharp angle from the others so as to produce a biramous climbing organ. This biramous character is very deep-seated and conspicuous in the foot of all known Primates from the Lower Eocene onward, and not even the foot of man, when carefully examined, is an exception to this rule. For although the great toe in man diverges but little from the other digits, the construction of both the bones and the muscles of the foot

³ R. W. Miner. *Bull. Amer. Mus. Nat. Hist.*, LI, Art. VII, 1925.

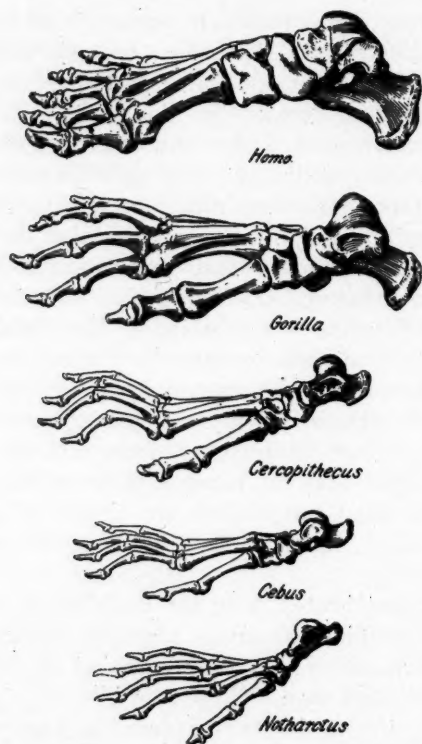


FIG. 7. Evolution of the foot in Primates. After Gregory.

suggests that it is merely a transformed biramous foot in which the first toe has been drawn forward so as to be nearly parallel with the others.

An important objection to the derivation of the human foot from a biramous Primate type is visualized in a figure by Professor Wood Jones, which shows the transverse deep metatarsal ligament in man tying the great toe firmly to the other digits, whereas in the gorilla, as here drawn, there is no such ligament.

My colleague, Mr. Raven, has shown, however, that in both the chimpanzee and the gorilla there is a strong transverse band of connective tissue in the web between

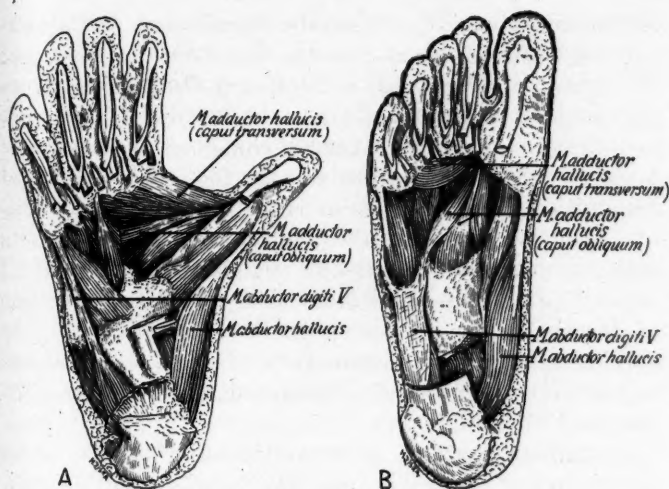


FIG. 8. Grasping muscles of the great toe and their opponents as seen in the sole of the foot in (A) Gorilla, (B) Man. After dissections by H. C. Raven.

the great toe and the second digit. A shortening and strengthening of this band, such as we may well suppose to have occurred in the ancestors of man, would produce a transverse metatarsal ligament.

In short, the longer and more intensively the anatomy, osteology and functioning of the parts of the human foot are studied, the more decisive is the evidence that the human foot is an anatomical palimpsest, bearing the clear traces of successive transformations of function and structure. To mention only a few of these, from the earliest period of the transformation of a radiating crossopterygian paddle into a five-rayed cheiropterygium, the human foot retains all five digits; from the early running stage of the ancestral mammals it retains, *inter alia*, the bony heel or lever on the calcaneum for the attachment of the tendo Achillis; from the earliest Primate stage the human foot retains distinct traces of a formerly biramous condition in which the great toe diverged sharply from the others; and from a primitive

anthropoid stage it retains the broadening and down-turning of the heel and even the dominance of the great toe over the others. The latest transformation, from the climbing anthropoid foot to the bipedal human foot, doubtless involved a great many changes throughout the muscles, bones and ligaments of the foot. The universal recognition of this particular transformation has doubtless been hampered by the tendency of paleontologists and morphologists to assume that such a specialized organ as the anthropoid foot could not on the principle of irreversibility give rise to the radically different specialization of the human foot. But strong evidence to the contrary has been discovered by Professor Elftman and Mr. Manter.

A striking example of transformation is offered by the history of the pelvis (recently discussed in this journal, May-June, 1935, Figs. 5-12), which had its early beginnings in the row of little rods that supported the pelvic keels or fins in the earliest true fishes. By the narrowing of the fin-fold at the base and the fusion of some of the proximal row of rods, such a fin was changed into a movable paddle. By the time of the Devonian lobe-finned or crossopterygian fishes the pelvis was represented by a pair of rods with posterior expansions around the cloacal outlet, embedded in the ventral body wall.

When the lobe-finned fishes came on land and began to use their paired fins as legs the pelvis developed a dorsal process, the future ilium, to which were attached in front the ilio-costalis muscles and in the rear the ilio-caudalis muscles. By this time the ribs in the future sacral region had begun to widen but they were not yet in contact with the ilium. In the early reptiles the sacral articulation was effected and the gluteal surface of the ilium began to expand. In the mammal-like reptiles the gluteal surface extended upward and forward, and in the early mammals the ilium became narrowed into a triquetrous rod with sacral, iliacus and gluteal surfaces.

By the time we reach the earliest known Primates the

iliac blade was everted laterally and soon afterward the ilium began that transverse expansion between the ilio-psoas and gluteal masses which culminates in the fan-like ilium of the gorilla. In man, however, there is an apparently sudden shortening of the vertical diameter and an extreme extension of the postero-superior border, which several authors have rightly correlated with the assumption of the upright posture.

On the medial side of the ilium the sacral articular surface in man often takes the form of a widely open U with the posterior longer than the anterior arm, as shown in the figure by Straus; whereas in the great apes this articulation forms an upward and forwardly inclined curved path. It is only in some of the Old World monkeys, especially the baboon, that one finds the posterior arm of the articular surface as well developed as the anterior arm. Therefore, argues Dr. Straus in essentials, by the law of irreversibility of evolution the sacral articular surfaces of the gorilla and chimpanzee are too much specialized to give rise to that of man and we must go down to the horizon of the Old World monkeys to find the common structural ancestor of the sacral surface of man and the anthropoid apes.

I, on the other hand, would suggest that this is a typical case of the unwarranted extension of the principle of irreversibility and that there is considerable direct evidence that the peculiar shape of the sacral articulation in man is a neomorph and that it has appeared *pari passu* with the great increase in size of his sacral vertebrae and especially with the development of the sharp lumbar curve in the vertebral column.

In the chimpanzee the lumbar curve is at most incipient. In man it eventually produces a sharp angulation between the upper part of the column and the sacrococcygeal region. This peculiar position of the suprasacral portion of the column, which is thus brought well in front of the sacrum, is compensated first by the backward and upward growth of the postero-superior blade

of the ilium; secondly, by the great widening and consolidation of the entire sacral platform; thirdly, by the extension and widening of the sacral articular surface, especially on its posterior side. The same factors condition the strong curving which culminates in the great sciatic notch.

I conclude, therefore, that the human pelvis has attained its present condition by a series of major transformations attending equally great shifts in locomotor habits and alternating with periods of apparently undeviating or progressive evolution.

The same two principles of undeviating evolution and transformation are likewise often apparent in the history

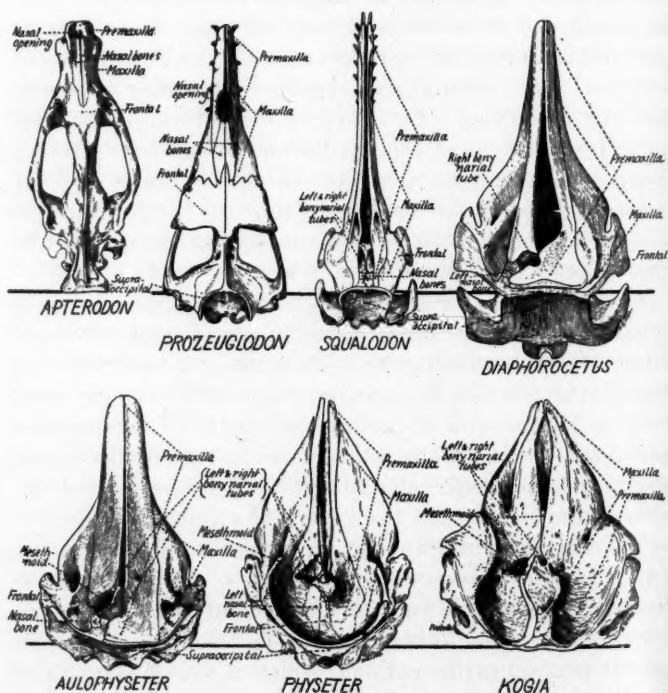


FIG. 9. Transformation culminating in the skull of the pygmy sperm whale. After Raven and Gregory.

of the skull of all known classes and orders of vertebrates. Undeviating evolution is particularly well shown in Professor Osborn's figure of the evolution of the skull in the *Mesatirhinus-Dolichorhinus* series of Middle and Upper Eocene titanotheres, in which the breadth index of the skull falls steadily from 53 to 43.

The other principle, that of transformation, is illustrated in the evolution of the skull of the sperm whale, as worked out in a paper by Mr. Raven and myself. While certain authorities exclude the Archeoceti from the ancestry of later whales, few could deny that in the top view the Eocene *Prozeuglodon* forms a structural intermediate between a primitive carnivorous mammal and the toothed cetaceans. The latter early shifted the bony nares to the rear and greatly lengthened the rostrum. But in the lines leading to the sperm whale and the pygmy sperm whale the bony rostrum shortened and widened, finally to an extreme degree.

In the evolution of the vertebrate skull from fish to man there have been so many major revolutions that it is no wonder that anatomists, often ignoring the materials supplied by paleontology, have sometimes failed to realize how, for example, the temporo-mandibular joint came into existence or by what steps the quadrate and articular bones of lower vertebrates were changed into the incus and malleus, respectively, of mammals.

A series of basal views of the skull, representing ascending grades of organization, shows the dominance of the primary or inner upper jaw in the lower vertebrates and its gradual retreat and dwindling before the advancing secondary or outer upper jaw in the mammal-like reptiles and lower mammals, culminating in the breaking-up of the primary upper jaw and the almost vestigial condition of the true pterygoids in the anthro-poids and man.

Both undeviating evolution and transformation have arisen from the combination of two great methods of ontogenetic and phylogenetic development, which I have

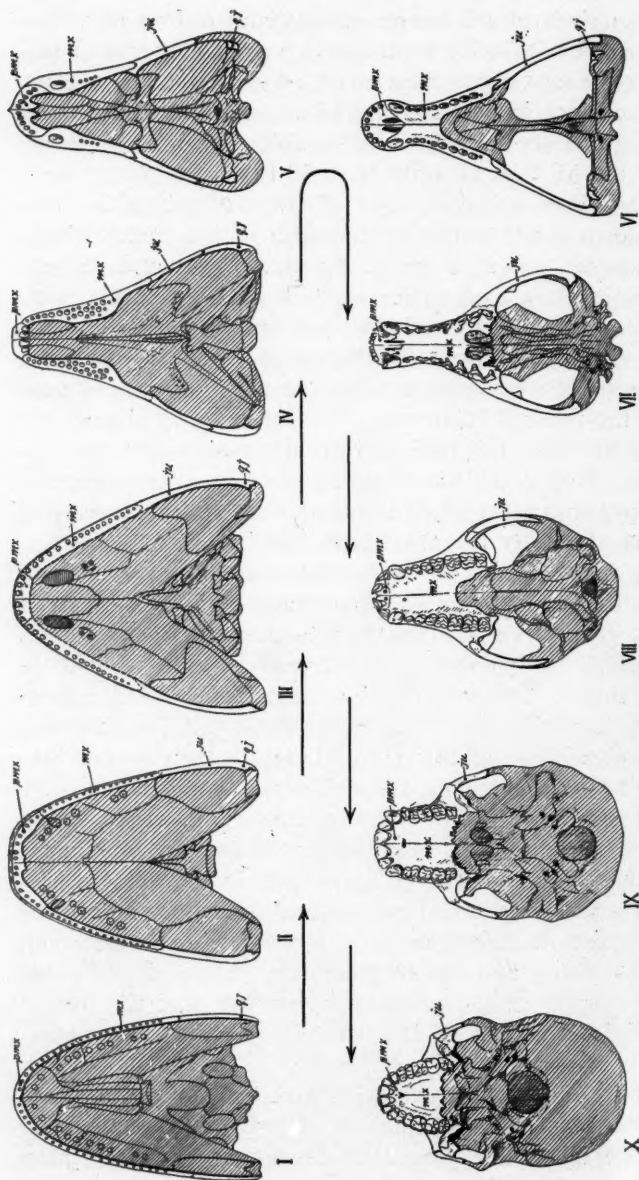


FIG. 10. Transformation of the upper jaws in vertebrates from fish to man, showing positive anisomerism of outer upper jaw (pmx, mx, ju). After Gregory.

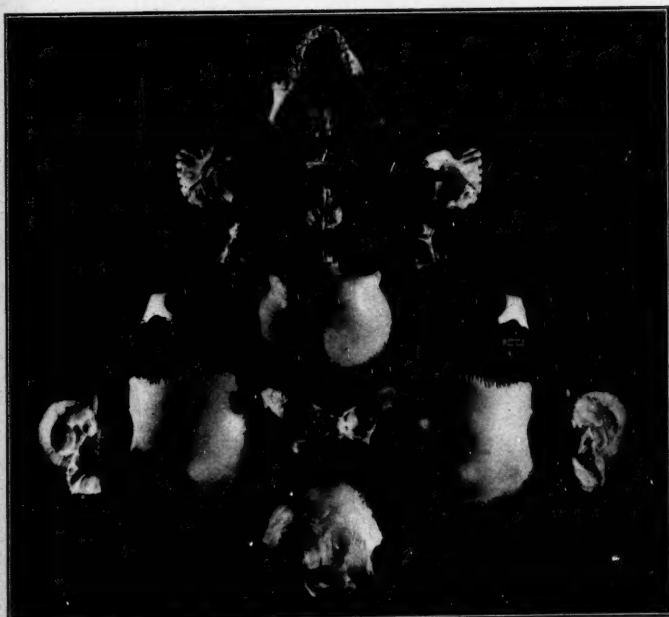
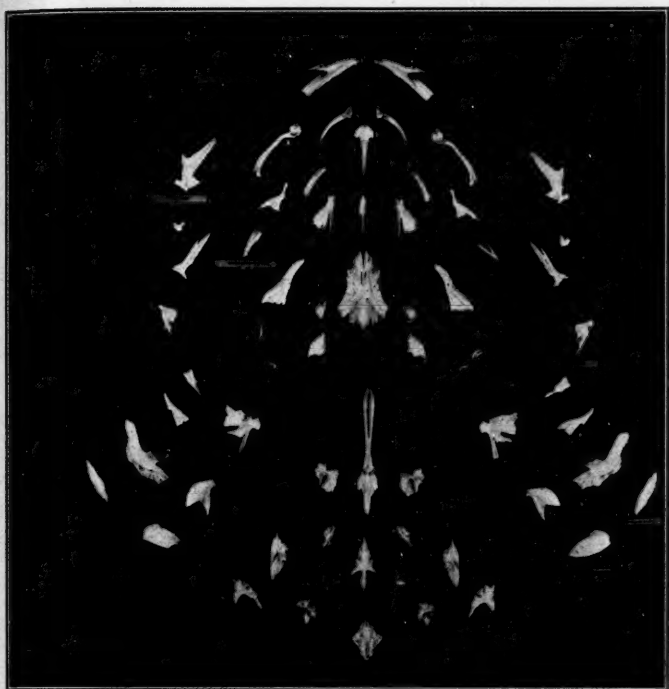


FIG. 11. Disarticulated skulls of cod and man, showing polyisomerism and anisomerism in cranial elements.

called polyisomerism and anisomerism. Polyisomerism corresponds partly to growth or reduplication, anisomerism to the selective increase or decrease of polyisomeres, either as wholes or along one or more of their axes. Thus in the most primitive lobe-finned fishes there are about 143 named bones in the skull and, on the whole, these bones differ less among themselves than they do in later types. In man, on the other hand, there are usually only 27 or 28 bones in the skull and the several parts are extremely unlike.

The late Professor S. W. Williston noted the tendency of vertebrate skulls to lessen the number of elements by reduction in size and eventual disappearance or by fusion of adjacent elements into larger groups. I have therefore called this phenomenon "Williston's Law" and with the aid of my research assistant, Miss Roigneau, and of several graduate students in Columbia University I have made careful lists of the skull bones present in fully adult representative samples of many recent and fossil vertebrates of all classes. The general results are summarized in this chart. The slight increase in the number of separate cranial bones in man is due to the emphasis and prolongation of infantile stages; so that this exception to irreversibility is more apparent than real.

The development of new bony centers, the fragmentation of old areas, the secondary delay in the closure of normal sutures or the selective prolongation of growth of a certain part, all disguise and complicate the picture and afford points of departure for new transformations.

A comparison of the mesial aspect of the left half of the skulls of chimpanzee and man indicates that the observed differences have resulted from a combination of undeviating evolution and of transformation. To the former category belong the enormous expansion of the braincase as a whole in man and the pushing up of the forehead into a nearly vertical wall by the forward growth of the temporal lobe of the brain. The transformation is seen in the sharp abbreviation of the entire

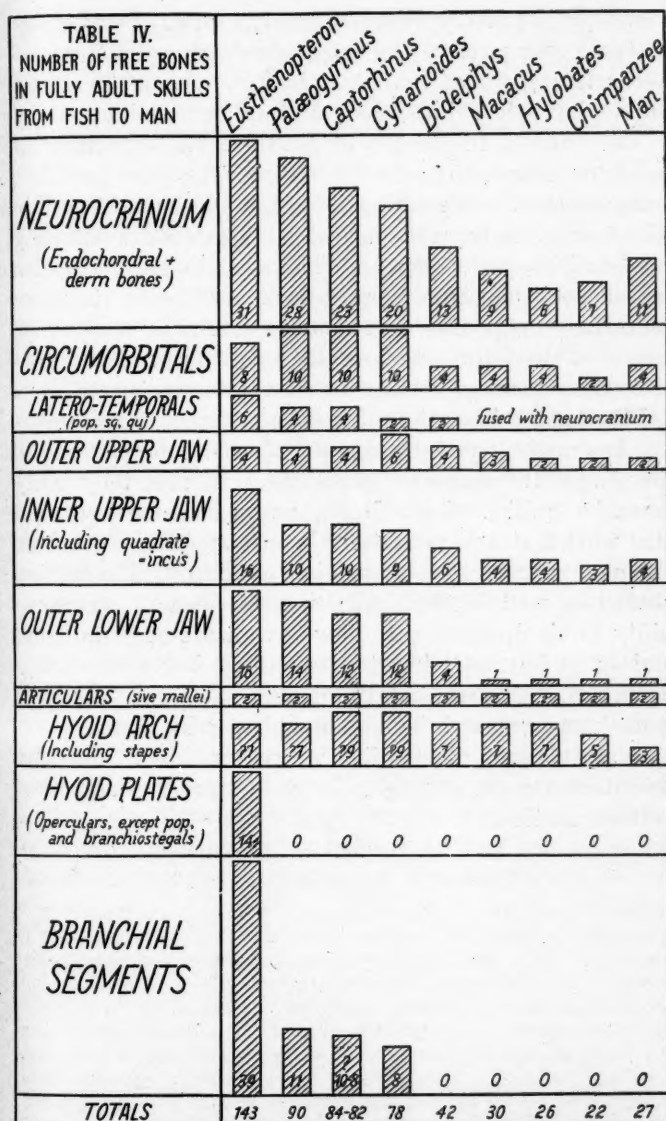


FIG. 12. Chart showing progressive reduction in number of skull bones from fish to man.

upper jaw in man, accompanied by a forward expansion of the upper part of the nasal chamber and the consequent lifting up of the nasal bridge. Assuredly if we did not have the chimpanzee we would have to invent him.

The fruitful researches of neurologists, especially of our honored guest, Professor Kappers, have revealed the combination of undeviating evolution and transformation which, starting from the lowest fish types, has eventually produced the brain of man. The neurologists have also traced the transition from paleokinesis, with its more immediate responses to sensory stimuli, to neokinesis, which in the later stages of the neopallium makes possible the control of conduct by ideas.

Finally, the invention of speech and verbalized thinking has made it possible for a leader to communicate to his people the magic of mass ideas, so that they jump when he speaks. Louis Dollo, a real leader, discovered that when a structural pattern is once modified it is never completely restored to its original condition. But he succeeded so well in communicating the idea of irreversibility to his disciples that they have made of it a dogma and have become blind to everything but undeviating evolution. An anthropoid foot, they say, *could not* have been transformed into a human foot. It is too much specialized and "Evolution is irreversible." Against this dogma I am willing to break a lance in defence of transformation.

ON THE DIMENSIONS OF CHROMOSOMES AND GENES IN DIPTERAN SALIVARY GLANDS

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THE theory of Koltzoff (1934), afterwards developed independently by Bridges,² that the so-called giant chromosomes of *Drosophila* salivary glands are hollow bundles of chromonemata, formed by the side-by-side proliferation and apposition of one original chromonema (or of two conjugated homologues), at once brings our conception of these structures into harmony with the known cytological and genetic facts concerning chromosomes in general. But the question is still asked by some: "Why should it be that these structures develop and are visible in the gland cells of *Drosophila* and other *Diptera* and do not seem to have been noted elsewhere?" The answer appears to be a very simple one and in fact, by the simplicity of the explanation it provides, it really constitutes a further corroboration of the Koltzoff-Bridges theory itself.

The answer is that, as was shown long ago by Stevens (1908) and others, *Diptera* differ from other organisms in the exceptional strength of the synaptic force acting between their homologous chromosomes and chromosome parts in non-meiotic stages. Whereas, in other animals and plants, the tendency of like genes to come together is little evident except at meiosis, in *Diptera* either this tendency remains stronger, or counter forces do not

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² Professor Koltzoff visited the Institute of Genetics in Leningrad in March, 1934, and at that time gave a lucid exposition of the essentials of his theory of the structure of the chromosomes in the salivary glands to members of the institute. The present author, convinced by Koltzoff's formulation, thereupon found a supporting fact in the longitudinal fibrillation which he had already noticed in Ellenhorn's photographs of the *Drosophila* salivary gland chromosomes, and pointed out that the number of elements visible in them in the transverse direction seemed to be a power of two (2⁴). Koltzoff's paper on the subject, which was sent in to press in America in April, 1934, was read by the present author at the time of sending.

develop so strongly, so that, wherever the chromosomes are visible, whether in somatic or germ cells, they show a strong tendency to conjugate. In the case of the salivary glands and other cells in which, through reduplication, numerous identical chromonemata have been formed, this synaptic affinity would tend to hold all these homologous parts together in groups (with their corresponding chromomeres in apposition so as to give the appearance of cross-striations).

It is probable, in accordance with the conception of the author (1922, *AMER. NAT.*, 56: 32-50) concerning the nature of the attractive force, and in accordance with the well-established findings and theories of Darlington, that this attraction is primarily two-by-two and is exerted more strongly along a certain plane. This would tend to result in primary, secondary, tertiary, etc., two-by-two associations, all in the same plane. But as the residual force between more and more distant, less directly conjugated strands is progressively weaker, this plane can bend sufficiently to allow its edges also to come into contact, *i.e.*, the strands must tend to arrange themselves endlessly around the periphery of a hollow cylinder. This periphery, then, represents the plane of the strongest attractive forces.

There is every reason to believe that essentially the same type of elongated chromonemal filaments as are seen in the "giant chromosomes" of *Diptera* exist also in the resting cells of other forms, although in these other forms the one important condition necessary for the grouping of these filaments into bundles is absent: namely, an attraction between like genes strong enough (despite insulating and repelling forces) to effect their apposition. Ever since the work of Bonnevie (1909) and of Vejdovsky (1911), there has been definite evidence that the uncoiling spirals (chromonemata) seen in the chromosomes at anaphase and telophase retain their continuity and persist in almost completely uncoiled condition throughout the resting stage, to reform the coils which are seen again in the prophase chromosomes. The

reason this did not receive earlier general recognition is because the irregular staining, extreme fineness and great length (with consequent repeated folding back) of these uncoiled chromonemata make it extremely difficult to follow out the course of the individual threads in the resting nuclei of ordinary fixed preparations, while in living material the refractive index of the threads is virtually identical with that of the nucleoplasm. As was pointed out by the present author in 1916 (*AMER. NAT.*, 50: p. 291), the newly discovered genetic facts of the persistence of the genes in unchanged linear order, throughout the entire reproductive life of the individual, and the evidence that even homologous loci do not undergo any exchange of positions until the meiotic period arrives, made it necessary to postulate the existence of the same structure as that observed cytologically by Bonnevie and Vejdosky, inasmuch as it had to be concluded that the genes are arranged in the form of a long fine persistent thread, and in order that such a gene-string might be present within the chromosomes at mitosis (as the genetic and cytological evidence combined in proving to be the case) it had necessarily to be coiled somehow. There was, therefore, no alternative to the geneticists, from accepting the chromonema theory of the more advanced cytologists.

On this now orthodox interpretation, then, the chromosomes in the resting stages of cells in general must have essentially the same structure as that seen in the salivary glands of *Diptera*, except that the chromonemata need not have become reduplicated, and have not become apposed. In regard to the matter of the reduplication of the strands, the distinction is not everywhere applicable. For it is probable that such a reduplication often occurs, in the somatic cells of other forms as well as of *Diptera*, especially when these cells are not destined for further division but (as so-called "noble cells") attain a large size in adaptation to some specific physiological function. As Koltzoff points out, evidence of such polyploidy has been obtained by Jacoby (1926) in the case of mammalian

liver cells. In other forms than Diptera, however, the existence of such polyploidy must only increase the tangle of separate chromonemata winding about through the nucleus and thus make an identification of the individual chromosomes even less possible, whereas in Diptera the active synaptic affinity leads to an orderly grouping of strands which allows us to recognize the chromosomes (or rather, the groups of chromonemata) as such. We see, then, that if the Bonnevie-Vejdovsky theory is right, the observed fact of a somatic conjugation in Diptera should lead us to expect the formation of the giant structures which we see, without our assuming any other unusual property of Diptera or of gland chromosomes.

We are now in a position to judge in what sense the chromosomes seen in the *Drosophila* salivary glands may really be considered "giant chromosomes." We have seen that their exceptional thickness is explained by the fact that they are compounded of a group of parallel identical chromonemata, and not merely compounded, but arranged in a *hollow* bundle so as to greatly increase the thickness of the group as a whole. Each individual chromonema, however, is probably no thicker in the "giant chromosome" than in the mitotic chromosome, though it may of course have accessory material around it. Nor is there ground for supposing that the individual chromonema is finer in the "giant chromosome," or in resting stages of cells in general, than it is in the mitotic chromosome: it appears thicker in the mitotic chromosome, but the existence of smaller coils within the larger coils, which would lend apparent thickness to the coiled threads of the mitotic stages, had been noted even by Vejdovsky. The same fact of coiling (coarser and finer) also explains readily the far greater apparent length of the strands in the salivary glands of Diptera, and in the resting stages of cells in general, than at mitosis. Hence there is no basis for postulating that the salivary gland chromosomes are really of a very different length than the chromonemata of the mitotic chromosomes (except, of course, when they have artificially been put

under tension).³ It is probable, then, that the "giant chromosomes" are giant only in appearance: essentially, they are chromonema-bundles, in which the structure of the individual chromonema is simply made more manifest by its (for us) convenient uncoiling, reduplication and accurate aggregation.

A few calculations regarding the sizes of the chromonema parts, based upon the premises stated above, may be of interest here. If we assume that the entire mass of the active region of the X chromosome of *Drosophila melanogaster*, as seen at metaphase in the oogonial cells, consists of tightly coiled chromonemal material, filling up all the space, and that this chromonema retains its same length and thickness in the salivary gland chromosome, then, by measurements of the chromosomes in these two stages and by a few simple calculations, it can easily be shown that (with some correction for shape) the average diameter of the chromonema, including that of the gene, in a direction transverse to the longitudinal axis of the chromonema, can not be more than 1/50th of a micron (.02 μ). (We say "average diameter," since it is improbable that the "breadth" and "thickness" of the chromonema are exactly equal). The above result is reckoned as follows:

$$\text{Volume of X at metaphase} = \text{length } (2 \mu) \times \text{breadth } (\frac{1}{2} \mu) \times \text{thickness } (\frac{1}{2} \mu) = \frac{1}{2} \text{ cu. } \mu.$$

$$\text{Volume of active region} = \frac{2}{3} \times \frac{1}{2} \text{ cu. } \mu = \frac{1}{3} \text{ cu. } \mu.$$

$$\text{Length in salivary gland (after Bridges)} = 200 \mu.$$

$$\text{Let average diameter} = x.$$

$$\text{Since volume} = \text{length} \times (\text{dia.})^2, \text{ we have } \frac{1}{3} = 200 x^2$$

$$x^2 = 1/2400$$

$$x = (\text{approx.}) 1/50 \mu. \text{ or } .02 \mu.$$

If, on the other hand, we assume that the metaphase chromosome does not have its entire volume occupied by the chromonema, but that the latter is tightly coiled about the periphery only, then the chromonema would

³ Even though the chromosome contraction for mitosis may involve some folding and coiling within the molecule itself as demonstrated by Astbury for keratin fibers, nevertheless the molecule itself is essentially a chain structure the length of which may be considered as its extended length with the secondary connections undone, and it is the length in this sense which we are considering in the above discussion.

have a thickness, in the direction parallel to the surface of the coil, of only 1/250th of a micron (*i.e.*, .004 μ). In this case we have reckoned as follows:

$$\begin{aligned} \text{Diameter of coil in metaphase chromosome} &= \text{thickness of metaphase chromosome} = \frac{1}{4} \mu. \\ \text{Length of one coil in metaphase chromosome} &= \pi \times \text{diameter of coil} \\ &= 3.14 \times \frac{1}{4} = .8 \mu \text{ (approx.)} \\ \text{Number of coils, each } .8 \mu \text{ long, in whole chromonema, } 200 \mu \text{ long,} \\ &= \frac{200}{.8} = 250. \end{aligned}$$

Since 250 coils must be crowded side by side within a distance of one micron (the approximate length of the active region at metaphase), the width of one coil must be about $\frac{1}{250} \mu$ or .004 μ .

Probably the truth lies in between these two calculations, but nearer to the first, in view of the fact that there are probably both primary and secondary and perhaps other coils. If the chromonemal coils are not in actual contact, however, their diameter must be correspondingly less.

We may proceed from the above to some tentative calculations concerning the genes. Suppose that the genes are as densely spaced (in the longitudinal direction) throughout the chromonema of the active region of the X as they have been found to be in the "second" band (Muller and Prokofyeva, 1934, 1935; Ellenhorn, Prokofyeva and Muller, 1935). The width (*i.e.*, chromonemal length) of that part of the "second" band containing the genes yellow, achaete, scute and the lethal to the right of scute is approximately .5 μ (as seen best in the ultra-violet photographs). There are probably very few, if any, other genes within the segment in question. This gives a length of approximately 1/8 micron for one gene, supposing—as seems probable, despite Belling—that there is little or no intergenic material in the longitudinal direction. According to this reckoning, then, the gene length would be between 6 and 30 times as great as its diameter (according to which of the above two estimates of the diameter is chosen). This is in agreement with the fact that proteins and other complex organic mole-

cules in general are chain-like, being much longer in one dimension than in the other two. We must, however, be careful of accepting these preliminary figures as coming even near to the actualities, in so far as we must bear in mind that several of the premises used in calculating them are by no means established and that the correctness of the conclusion as a whole depends upon the correctness of all the premises simultaneously. We are, however, on safer ground in taking the maximal figures for length and breadth as giving the maximum possible gene and chromonemal dimensions. And we see that, even taking these maxima, the *volume* of the gene is much too small to allow it, by itself, to give a visible image—although, on account of its tenuity, its *linear* extent may be just within the visible range. This agrees with the conclusion expressed by the author in 1922 (AMER. NAT., 56, *ibid.*).

The chromonema, too, turns out to be too fine to give an image, except by diffraction or by aid of the accumulation of accessory material about it. We have in the above calculated it to be between $1/50$ and $1/250$ of a micron in diameter. But the salivary gland X-chromosome has a periphery of about $12\frac{1}{2} \mu$ (3μ diameter $\times \pi$). If, as we should judge from the appearance of ordinary preparations, by visible light, there are only 16 fibrils in it, this gives a space of $\frac{1}{4} \mu$ for the diameter of each fibril, together with its accessory material. The above calculated fineness of the individual fibril, however, makes it impossible to say, on the basis of simple observation, how many actual fibrils may be represented within one apparent fibril, and, if there is a basic two-by-two grouping, this would be expected to give an appearance of secondary fibrils, similar in arrangement to the individual ones. Ultra-violet photographs, as well as studies of nuclear growth, may throw some light upon this problem; the former have already indicated a more compound structure than was evident in visible light, but can not yet be regarded as conclusive, since in such light, too, diffraction images may occur.

INFLUENCE OF TEMPERATURE ON TESTIS SIZE IN *DROSOPHILA PSEUDOÖBSCURA*

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RACES A and B of *Drosophila pseudoöbscura* Frolova produce sterile male hybrids when crossed. Male offspring of the cross B ♀ × A ♂ have testes visibly smaller than normal. F₁ hybrid females, when back-crossed to males of parental races, produce sons having testes of variable size—from normal to very small. Individuals having small testes are sterile (Dobzhansky and Boche, 1933). Spermatogenesis is highly abnormal in males having small testes (Dobzhansky and Boche, 1933; Dobzhansky, 1934), the degree of abnormality being inversely proportional to testis size. It has also been noticed by Dobzhansky (1934) that temperature affects the size and structure of testes in hybrid males, high temperature making testes smaller and spermatogenesis more abnormal, while low temperature has the reverse effect.

Experiments were undertaken to study the effects of temperature in more detail. In the first series of experiments females of pure races (La Grande-2 and Texas of race A, Seattle-6 and Seattle-4 of race B) were mated to males of the same species and allowed to oviposit for twelve hours in the same bottle at 25° C., after which they were transferred to fresh bottles and allowed to oviposit there for the same interval of time and at the same temperature. The bottles with the eggs thus secured were put in incubators at 16° C., 20° C., 24° C. and 28° C., and left there for the entire time of development. Similar experiments were arranged with hybrids from Seattle-6 ♀ × La Grande-2 ♂ and Seattle-4 ♀ × Texas ♂ (Seattle-6 and Seattle-4 are race B, La Grande-2 and Texas race A).

When flies emerged in the culture bottles, males were dissected and their testes measured with the aid of an eyepiece micrometer (one unit equal to 17.4 micra) in a drop of physiological salt solution. Length and width were measured, the method of measurement being the same as that used by Dobzhansky and Boche (1933). The results of the measurements on length are presented in Table 1.

TABLE 1

LENGTH OF TESTES IN SOME PURE RACES OF *D. PSEUDOÖBSCURA* AND THEIR HYBRIDS DEVELOPED AT GIVEN TEMPERATURES (IN MICRA)

Cross	t°	M ± m	σ	Lim	n
La Grande-2 ♀	28	528.5 ± 8.9	63.0	400.5-649.7	50
×	24	800.8 ± 6.5	46.2	694.2-890.0	50
	20	806.3 ± 6.6	46.5	720.9-961.2	50
La Grande-2 ♂	16	878.4 ± 6.6	46.7	774.3-996.8	50
Seattle-6 ♀	28	436.2 ± 17.3	93.7	275.9-676.4	50
×	24	692.2 ± 7.1	50.7	569.6-792.1	50
	20	793.4 ± 6.4	45.7	694.2-934.5	50
Seattle-6 ♂	16	794.4 ± 6.5	46.2	694.2-907.8	50
Texas-♀	28	471.9 ± 9.8	69.4	373.8-623.0	50
×	24	717.2 ± 5.5	39.3	605.2-792.1	50
	20	781.3 ± 5.1	35.8	685.3-854.4	50
Texas-♂	16	835.2 ± 4.2	37.1	738.7-907.8	50
Seattle-6 ♀	28	159.1 ± 7.8	28.3	106.8-204.7	13
×	24	374.6 ± 10.7	117.2	169.1-720.9	121
	20	481.6 ± 6.9	98.0	240.3-720.9	200
La Grande-2 ♂	16	528.8 ± 6.0	89.2	275.9-809.9	224
Seattle-4 ♀	28	101.2 ± 7.0	27.3	44.5-151.3	15
×	24	197.9 ± 4.0	40.6	124.6-320.4	100
	20	383.3 ± 5.0	71.3	195.8-578.5	200
Texas-♂	16	410.8 ± 5.0	71.3	231.4-658.6	200

The temperature at which development takes place (t°), mean values with their mean error (M ± m), standard deviation (σ), limits of variation (Lim) and number of individuals tested (n) are given. The measurements on width show a similar variation, and are omitted here. The temperature of 28° C. is generally

lethal for *D. pseudoöbscura*. Some flies develop up through the pupal stage but fail to emerge. Testis measurements on flies developed at this temperature were made by dissecting apparently mature pupae.

It is evident that testis size is highly sensitive to temperature, especially in the hybrids, but also in the pure races. The hybrid testes are nearly four times as large at 16° C. as at 28° C. The temperature change from 24° C. to 28° C. produces an especially marked effect. As stated above, 28° C. is close to lethal.

TABLES 2 AND 3

LENGTH OF TESTES IN LAGRANDE-2 EXPOSED TO HIGH TEMPERATURE AT SUCCESSIVE STAGES IN DEVELOPMENT. IN TABLE 2 EXPOSURE WAS FOR TWENTY-FOUR HOURS AT 27.6° C.; IN TABLE 3 EXPOSURE WAS FOR EIGHT HOURS AT 28.4° C. (IN MICRA)

	Age in days at time of treatment	M + m	σ	Lim	n
TABLE 2	1 - 2	806.7 \pm 4.4	43.7	696.0 - 904.8	100
	2 - 3	778.1 \pm 4.9	48.6	696.0 - 922.2	100
	3 - 4	784.9 \pm 4.4	43.7	661.2 - 887.4	100
	4 - 5	790.0 \pm 5.1	50.6	661.2 - 904.8	100
	5 - 6	780.2 \pm 5.1	51.3	678.6 - 870.0	100
	6 - 7	763.0 \pm 5.3	53.1	626.4 - 870.0	100
	7 - 8	723.2 \pm 7.7	76.9	348.0 - 852.6	100
	8 - 9	771.9 \pm 6.1	60.9	574.2 - 870.0	100
	9 - 10	757.6 \pm 6.7	66.6	574.2 - 887.4	100
	10 - 11	746.3 \pm 5.5	55.2	522.0 - 887.4	100
	11 - 12	763.3 \pm 4.9	48.7	661.2 - 852.6	100
	11 - 12	754.1 \pm 6.1	60.7	609.0 - 870.0	100
	Control	789.4 \pm 4.0	39.5	678.6 - 887.4	100
	5 $\frac{1}{2}$ - 6	743.0 \pm 11.5	74.5	522.0 - 887.4	42
TABLE 3	6 - 6 $\frac{1}{2}$	734.5 \pm 8.5	67.0	522.0 - 852.6	62
	6 $\frac{1}{2}$ - 6 $\frac{3}{4}$	732.4 \pm 11.0	74.8	487.2 - 887.4	47
	6 $\frac{3}{4}$ - 7	730.8 \pm 12.3	80.2	382.8 - 870.0	42
	7 - 7 $\frac{1}{4}$	723.0 \pm 9.6	68.7	522.0 - 852.6	51
	7 $\frac{1}{4}$ - 7 $\frac{1}{2}$	703.0 \pm 9.7	77.8	504.6 - 852.6	64
	7 $\frac{1}{2}$ - 8	667.8 \pm 8.4	58.3	539.4 - 783.0	50
	8 - 8 $\frac{1}{4}$	717.6 \pm 8.2	64.0	522.0 - 835.2	62
	8 $\frac{1}{4}$ - 8 $\frac{3}{4}$	720.4 \pm 7.0	48.2	626.4 - 852.6	48
	8 $\frac{3}{4}$ - 9	734.1 \pm 7.8	56.6	626.4 - 852.6	53
	Control	798.7 \pm 4.2	41.6	678.6 - 904.8	100

In the second series of experiments it was attempted to find a sensitive period for the effect of temperature on testis size. Cultures with eggs freshly deposited at 25° C. were secured by the method described above. La Grande-2 stock (race A) was used throughout. Some of the cultures were allowed to develop at 25° C. till flies had emerged. These cultures served as control. The twelve groups of cultures, representing twenty-four-hour stages of development from egg to time of emergence, were simultaneously incubated at 27.6° C. for a period of twenty-four hours. The results of testis measurements are shown in Table 2.

The most marked decrease in length is obtained in flies which have been treated on the seventh day, or the period of development in which the prepupal stage is being entered. However, there is evidence of some effect earlier, since all groups in the series treated after the fifth day have testes smaller than in the control. In a group of experiments performed later (Table 3) it was attempted to more accurately locate a sensitive period in development. The interval between the fifth and ninth days was tested. Flies were allowed to oviposit for periods of eight hours only. The subsequent incubation period consisted of an exposure of eight hours also, but at a temperature of 28.4° C. Before and after exposure development took place at 25° C. As shown in Table 3, the most marked decrease in length occurs in that group exposed during the last third of the seventh day. The group immediately preceding shows the next most marked effect, indicating that some larvae were influenced by the middle of the seventh day. It seems significant here that all groups in this series have testes markedly shorter than the control. Hence, the increase of .8° C., even though employed for only one third the time used for 27.6° C., has decreased the average length for all stages tested. The percentage of dying pupae was undoubtedly higher in all cultures exposed to 28.4° C.

The behavior of the chromosomes during spermatogenesis in heat-treated males has not been traced in detail, but preliminary investigation has indicated that aberrations sometimes occur. At diakinesis it appears that non-disjunction may occur in a manner similar to that found in hybrid forms.

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THE INHERITANCE OF ACQUIRED CHARACTERS AND THE PROVISIONAL HYPOTHESIS OF PANGENESIS

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I

THE belief in the inheritance of acquired characters has been associated so consistently with the Chevalier de Lamarck that we now refer to it as Lamarckian, although Lamarck was neither the first nor the most distinguished biologist who taught that such modifications were heritable. Other and earlier naturalists had expressed very similar views, which, in the absence of rival hypotheses, were accepted by their contemporaries almost as a matter of course. Unfortunately, in our oversimplification of the history of biological thought, we have neglected the greater part of these earlier contributions and have consequently emphasized Lamarck's explanation of the causes of evolution out of all proportion either to its originality or to its intrinsic worth. As a result of this neglect of Lamarck's predecessors, modern biologists are periodically rediscovering the work of some one of these forgotten naturalists and finding anew that Lamarck's hypothesis is really pre-Lamarckian.

We can date Lamarck's conversion to a belief in evolution within a very few years. In 1795 he finally published his "*Recherches sur les causes des principaux faits physiques*," a book which he had completed in 1760, and in which he stated very clearly his belief in the immutability of species. Within the next seven years, however, his views underwent a complete reversal, for in 1802 he published his "*Recherches sur l'organisation des corps vivants*," and in this later work he presented his theory of evolution. Seven years later, in 1809, he published "*Philosophie zoologique*," which contained the

fully developed theory, and, although he often restated his concept of evolution, he never actually changed it. The following condensed statement of his four well-known "laws" is taken from his "*Histoire naturelle*" (as quoted by Osborn, 1894):

1. Life by its internal forces tends continually to increase the volume of every body that possesses it, as well as to increase the size of all its parts, up to a limit which it brings about.
2. The production of a new organ or part results from a need or want, which continues to be felt, and from a new movement which this need initiates and causes to continue.
3. The development of organs and their force or power are always in direct relation to the employment of these organs.
4. All that has been acquired or altered in the organization of individuals during their life is preserved by generation, and transmitted to new individuals which proceed from those which have undergone these changes.

The question has naturally been raised as to the cause of Lamarck's sudden acceptance of evolution and as to the source of his explanation of the factors which brought it about. The fact that Erasmus Darwin had described the inheritance of acquired characters in his "*Zoonomia*," 1794, published during Lamarck's transition period, has caused biologists to suspect that Lamarck borrowed his ideas from Darwin and that he simply failed to give credit where credit was due. In the chapter on "Generation" Darwin had stated, ". . . all animals undergo transformations which are in part produced by their own exertions in response to pleasure and pain, and many of these acquired forms or propensities are transmitted to their posterity," an exact statement of Lamarck's convictions. Osborn (1894) has shown very convincingly, however, that Lamarck was probably ignorant of Darwin's work, and he suggests that Lamarck's changed viewpoint was brought about by the shifting of his interests from botany to zoology, a reasonable enough supposition when we consider the emphasis Lamarck placed on functional modification and on the effects of use and disuse, factors which could hardly in-

fluence the development of plants, although plants were also thought to have evolved.

Recently Chevalier (1932) has called attention to a passage in the work of the little-known botanist, Michel Adanson, which is very significant, for it shows that Lamarck may have received his first hint as to the cause of evolution from his earlier work in botany rather than from his later interest in zoology. Adanson was Lamarck's predecessor at the Jardin Royal, and Lamarck could hardly have remained unfamiliar with Adanson's publications. Adanson not only described evolution in his "Familles de plantes," published in 1763 when Lamarck was a young man of twenty, but also suggested that the changes in specific characteristics were produced through the inheritance of acquired characters. The following two excerpts from his work are taken from Chevalier's paper:

It appears therefore to be proved sufficiently by the facts cited above that art, cultivation and especially chance, *i.e.*, certain unknown conditions, bring forth every day not only varieties of rare flowers such as Tulips, Anemones, Ranunculi, etc. . . . but even some new species. . . . From this arises the difficulty of defining what the original forms of the Creation are and what are those which have been changed by the succession of reproduction. . . .

The inheritance of acquired characters is postulated in the following:

In plants which reproduce by seed, there occurs, without the aid of alien impregnation, changes produced either by the reciprocal fertilization of two individuals, differing in some one character although of the same species, or by the cultivation, soil, climate, dryness, moisture, shade, sunlight, etc. These changes are more or less sudden, more or less durable, either disappear in each generation or *perpetuate themselves for several generations*, according to the nature, disposition and habit, so to speak, of each plant.

It is highly probable that we will never know just where Lamarck first met with the ideas for which he became famous, but we can understand his intellectual background better and we can evaluate his contribution to biology more accurately if we remember, first, that the belief in the inheritance of acquired characters does not

necessarily imply a belief in the evolution of new species and, second, that for at least 2,200 years before Lamarek practically all naturalists believed that such modifications were heritable. Not only such fantastic writers as De Maillet but also the most respected leaders and authorities postulated that the effects of environmental changes were inherited.¹ It would be tedious to cite here the numerous passages which would prove the correctness of this assertion. A single example taken from the "Opus Majus" of Roger Bacon will be sufficient, for it illustrates very clearly the attitude of the medieval philosophers toward the question. The "Opus Majus" was written in the year 1268.

Bacon tried to account for the fact that men no longer lived to the alleged ripe old ages of the antediluvian Patriarchs. The Astrologers, whom he attacked, had claimed that the stars were at the most advantageous positions possible at the time of the creation, and that as time passed they moved to other and more unfavorable locations. As a result, human life was shortened—and the race became more and more "ill-starred." Bacon attempted to refute this claim by advancing what he thought was a more reasonable hypothesis to explain the same undoubted facts. The following excerpt is from Chapter XII, Example 11, as translated by R. R. Burke (1928):

... Very rarely does it happen that anyone pays sufficient heed to the rules of health. No one does so in his youth, but sometimes one in three thousand thinks of these matters when he is old and approaching death, for at times he fears for himself and thinks of his health. But he cannot then apply a remedy because of his weakened powers and sense and his lack of experience. Therefore fathers are weakened and beget weak sons with a liability to pre-mature death. Then by neglect of the rules of health the sons weaken themselves, and thus the son's son has a doubly weakened constitution, and in his turn weakens himself by a disregard of these rules. Thus a weakened constitution passes from father to sons, until a final shortening of life has been reached as is the case in these days.

Not only is there this accidental cause, but there is also another, consist-

¹ In part II many passages will be quoted which establish incidentally the accuracy of this statement.

ing in the disregard for morals. For sins weaken the powers of the soul, so that it is incompetent for the natural control of the body; and therefore the powers of the body are weakened and life is shortened. This weakening passes from father to son, and so on. Therefore owing to these two natural causes the longevity of man of necessity has not retained its natural course from the beginning; but for these two reasons the longevity of man has been shortened contrary to nature. Moreover, it has been proved that this excessive shortening of the span of life has been retarded in many cases, and longevity prolonged for many years by secret experiments. Many authors write on this topic. Wherefore this excessive shortening of life must be accidental, with a possible remedy.

If we wish to trace the slow growth of our modern conception of evolution, we shall have to search intensely for those few pre-Lamarckian pioneers who did *not* believe in the inheritance of acquired characters. In the present state of our knowledge of biological history of course, we have no way of estimating the approximate number of such individuals. They may be more numerous than we suspect, although Brock (1888), who seems to have had a very clear grasp of the problem, found but two. These were (1) an unknown contemporary editor of Aristotle's works, and (2) the philosopher, Immanuel Kant. An investigation of our available records would doubtless reveal many others.

Aristotle himself believed implicitly in the inheritance of acquired characters, as is shown from the following passage in his "Generation of Animals," I: 17 (translated by Platt, 1910):

And these opinions are plausibly supported by such evidences as that children are born with a likeness to their parents, not only in congenital but also in acquired characteristics; for before now when the parents have had scars, the children have been born with a mark in the form of a scar in the same place, and there was a case at Calcedon where the father had a brand on his arm and the letter was marked on the child, only confused and not clearly articulated.

It would be hard to find a clearer statement of Lamarck's views. Aristotle, however, did not believe that mutilations were always inherited. From I: 18:

If mutilated young are born of mutilated parents, it is for the same reason as that for which they are like them. And the young of mutilated

parents are not always mutilated, just as they are not always like the parents; the cause of this must be inquired into later, for this problem is the same as that.

Aristotle's "History of Animals" bears internal evidence of having been thoroughly edited, perhaps by one of his own students. In this work there is a passage which corresponds with those quoted from the "Generation of Animals," but it has been toned down considerably. The influence of the unknown editor is clearly shown in the second paragraph of the following quotation. From VIII: 6 (translated by Thompson):

From deformed parents come deformed children, lame from lame and blind from blind, and speaking generally, children often inherit anything peculiar to their parents and are born with similar marks such as pimples and scars. Such things have been known to have been handed down through three generations; for instance, a certain man had a mark on his arm which his son did not possess, but his grandson had it in the same spot though not very distinct.

Such cases, however, are few; for the children of cripples are mostly sound, and there is no hard and fast rule regarding them.

Immanuel Kant was much more outspoken in his opposition to the belief in the inheritance of acquired characters. In his *Bestimmung des Begriffs einer Menschen-Race*, first published in the *Berlin. Monatsschr.* (6: 390) in 1785, he stated the theory only to refute it, although his refutation was based entirely upon *a priori* grounds. In Number 5 he stated (the translation is very free):

The inheritance through the working of the imaginative powers of pregnant women or even of mares at stud: the forcing of nature to omit gradually a product of her generation by the plucking out of the beards of whole tribes and by the cropping of the tails of English horses; the flattened noses, which had originally been bestowed with great pains by parents on their children, had consequently been given by the generative forces of nature: these and other explanations would scarcely be proven by the facts tending to substantiate them, for one can much better prove the contrary true, if they did not receive the reason for their existence from the otherwise entirely correct maxim, namely, it is preferable to risk everything in conjecturing from the given phenomena rather than to assume for this purpose special natural forces or innate "Anlage." But I urge another maxim, contrary to the above, which has generally been rejected through the neglect of this principle, namely, that in the entire organization of nature,

in spite of all variations, individual creatures of the same species remain essentially unaltered. Now it is clear that if the magic power of development or the experiments of men on animal bodies could bring about the possibility of altering the generative power, one would not know any more from which origin in nature any form may have come, whether the primitive form made by nature had persisted to the present or how far through additions or disfigurements it may have been modified, and, since there are no limits to the human imagination, into what grotesque shape the genera and species might at last grow. According to this consideration I take for my basic postulate, that we cannot admit that the bungling influence of the power of the imagination may affect the natural process of generation, or that any power of man through outer artificial modifications may affect the old original forms of the genera or species.

The third author quoted by Brock was Johann Friedrich Blumenbach, a physician. Blumenbach seemed unable to decide whether he should accept the heritability of acquired characters or not. In "*De generis humani varietate nativa*" (Göttingen, 1795) he carefully compared both views but leaned strongly toward the view that such characters were inherited. The following passage is translated from Brock's citation:

Until the present I join neither of the two parties, neither the adherents nor the opponents of this theory of heredity, although I would indeed make the view of the latter my own, if they could show me, why such developmental accidents, which next arise either through design or chance, could in no way be transmitted to the descendants, while indeed other racial characters from still other unknown sources, especially such as are stamped on the face, such as the nose, lips, eyebrows, etc., have been inherited until the present; in certain families, through many or few generations with greater or less clearness and even such characters as organic illnesses, defective speech and bad enunciation and many more like afflictions have been inherited, if they would not ascribe perhaps all of these defects only to chance.

In his "*Elements of Physiology*" (Philadelphia, 1795), he even endorsed the heritability of mutilation. From p. 182, Number 598:

It is necessary further to observe, that not only monstrosities co-eval with the birth of animals, but also subsequent adventitious mutilations and other species of deformity, whether produced on the animal system by accident or design, become now and then completely hereditary; and thus, what was at first the effect of art alone, may be said to become at length the actual work of nature herself.

We will probably never discover just where Lamarek first met with the hypothesis that acquired characters were heritable. It seems obvious now that he could not have read the biological literature of his time and remained in ignorance of the doctrine. His belief in evolution was also to some extent a product of his age, for, as Osborn has shown, the mutability of species had been suspected from the time of the ancient Greeks and many of the intellectual leaders were avowed evolutionists. One aspect of the history of evolution has never been properly emphasized, however, and the result has been that we do not view the subject with quite the proper perspective. It is important that we remember that the *dogma of the constancy of species is not an ancient doctrine and that it met with general acceptance only in the late eighteenth and the early nineteenth centuries*. From the earliest times, of course, sporadic individuals had taught that species were immutable, but their teachings had relatively little influence.² From the time of Theophrastos (300 B. C.) until the late eighteenth century, almost without exception the botanists believed in *degeneration*. Very few of their names have gotten into the evolution story, however, and even the meaning of the term *degeneration* is generally misunderstood.

Originally, degeneration had no connotation of decline or decay. It was simply the term used to describe the spontaneous alteration of varieties and species and thus it was synonymous with what we now call De Vriesian mutation. As this subject is being treated elsewhere no passages need be quoted to illustrate this ancient explanation of the origin of species.³ It is only necessary to

² Belief in this mutability of species was not necessarily a belief in the evolution of complex types from simpler predecessors.

³ Degeneration is described in the following passages: Theophrastos (*Caus. Plant.* I: 13), Virgil (*Georgics* I: 154), Nicolaus Damascenos (*De Plantis*), St. Augustine (*Mar. & Conc.* I: 21, I: 37), Crescentius (*Opus rural.* II: 8, II: 9), Porta (*Mag. Nat.*), Lemnius (*Ocul. Nat. Mirac.* I: 17), Clusius (*Rar. aliq. Stirp.* 513, *Rar. plant. hist.* 279), Gerard (*Herbal*, 116), Johnson (*Gerard's Herbal*, 740), Ferrario (*Flor. Cult.* 347), Worm (*Museum Worm*),

point out that during this whole period species were considered to be mutable and indeed were thought to be constantly changing, although the changes were not always looked upon as progressive and cumulative. Even as late as the time of Lamarck, the botanists were reporting instances of degeneration in the vegetable realm.

II

The "provisional hypothesis of pangenesis" was the name given by Charles Darwin to his least fortunate venture into speculation. After the publication of the "Origin of Species," Darwin leaned more and more toward a belief in the inheritance of acquired characters, and he advanced this hypothesis in an attempt to explain just how such somatic modifications could be transmitted from one generation to another. The following passage from chapter twenty-seven of his "Animals and Plants under Domestication" contains the entire hypothesis in a condensed form:

... But besides this means of increase I assume that cells, before the conversion into completely passive or "form-material," throw off minute granules or atoms, which circulate freely throughout the system, and when supplied with proper nutriment multiply by self-division, subsequently becoming developed into cells like those from which they were derived. These granules for the sake of distinctness may be called cell-gemmules or, as the cellular theory is not fully established, simply gemmules. They are supposed to be transmitted from the parents to the offspring, and are generally developed in the generation which immediately succeeds, but often transmitted in a dormant state during many generations and are then developed. Their development is supposed to depend on their union with other partially developed cells or gemmules which precede them in the regular course of growth. Why I use the term union will be seen when we discuss the direct action of pollen on the tissues of the mother plant. Gemmules are supposed to be thrown off by every cell or unit, not only during the adult state, but during all the stages of development. Lastly, I assume that the gemmules in their dormant state have a mutual affinity for each other, leading to aggregation either into buds or into sexual elements. Hence, strictly, it is not the reproductive elements, nor the buds, which generate new organisms,

Sharrock (*Hist. Propag.* I: 5), Morison (*Plant. Hist. Univ. Oxon* I: 205), Ray (*Hist. Plant.* I: 21), Hauser (*Thes. Bot.*, 25), Stehelin (*De flor. Peloria*), Nonne (*Quae. de plant. nothis*). These references are, of course, but a small fraction of an enormous literature.

but the cells themselves throughout the body. These assumptions constitute the provisional hypothesis which I have called Pangenesis.

Darwin knew that certain biologists had already suggested hypotheses very like his own, but he endeavored to emphasize the differences rather than the fundamental likenesses in these speculations. He recognized specifically the resemblances of Herbert Spencer's⁴ "physiological units" to gemmules, and he stated in a footnote that Professor Huxley had called his attention to the work of Bonnet and Buffon. Bonnet had advanced the theory of *emboîtement*, i.e., that the germs which were to form the next generation contained in themselves germs which were to form the third generation and so on to the end of the world. These germs were not, so to say, wrapped in cotton-wool, but could be reached supposedly by the "animal spirit" of the parent.⁵ On the other hand,

⁴From Chapter VIII of Spencer's "Principles of Biology," London, 1865.

"... It involves a denial of the persistence of force to say that A may be changed into A', and may yet beget offspring exactly like those it would have begotten had it not been so changed. That the change in the offspring must, other things equal, be in the same direction as the change in the parent, we may dimly see is implied by the fact, that the change propagated throughout the parental system is a change towards a new state of equilibrium—a change tending to bring the actions of all organs, reproductive included, into harmony with these new actions. Or, bringing the question to its ultimate simplest form, we may say that as, on the one hand physiological units will, because of their special polarities, build themselves into an organism of a special structure; so, on the other hand, if the structure of this organism is modified by modified function, it will impress some corresponding modification on the structures and the polarities of its units. The units and aggregate must act and re-act on each other. The forces exercised by each unit on the aggregate and by the aggregate on each unit, must ever tend towards a balance. If nothing prevents, the units will mould the aggregate into a form in equilibrium with their pre-existing polarities. If contrariwise, the aggregate is made by the incident actions to take a new form, its forces must tend to re-mould the units into harmony with this new form."

⁵This animal spirit has a certain remote resemblance to the gemmules. From Bonnet's "Oeuvres d'Histoire Naturelle," V: 7 (1781): "Thus I conceive that the animal spirit is carried by the nerves of the mother into her ovaries and that it is at first distributed to the most developed germs. I shall call these germs, the germs of the first generation or of the 'first

Buffon had postulated that the germ-plasm had collected first in the various body organs and only later passed to the testes or ovaries. The very close resemblance of Buffon's theory to Darwin's is shown by the following quotation from his "History of Animals" (Chapter IV):

The generation of man will serve us for an example. I take him in his infancy, and I conceive that the expansion and growth of the different parts of the body being made by the intimate penetration of organic molecules analogous to each of its parts, all these organic molecules are absorbed in his earliest years, and serve only for the expansion and the augmentation of his various members, consequently there is little or no superfluity until the expansion is entirely completed; and this is the reason why children are incapable of propagation; but when the body has attained the greatest part of its growth, it begins to have no longer need of so great a quantity of organic particles, and the superfluity, therefore, is sent back from each part of the body into the destined reservoirs for its reception. These reservoirs are the testicles and seminal vessels, and it is at this period that the expansion of the body is nearly completed, when the commencement of puberty is dated, and every circumstance indicates the superabundance of nutriment; the voice alters and takes a deeper tone; the beard begins to appear, and the other parts of the body are covered with hair; those parts which are appointed for generation take a quick growth; the seminal liquor fills the prepared reservoirs, and when the plentitude is too great, even without provocation, and during the time of sleep, it emits from the body. In the female this superabundance is more strongly marked, it discovers itself by periodical evacuation, which begin and end with the faculty of propagating, by the quick growth of the breasts, and by an attraction in the sexual parts, as shall be explained.

I think, therefore, that the organic molecules, sent from every part of the body into the testicles and the seminal vessels of the male, and into the ovarium of the female, form there the seminal liquor, which is, as has been observed, in both sexes, a kind of extract of every part of the body. These organic molecules, instead of uniting and forming an individual, like the one in which they are contained, commonly unite when the seminal liquors of the two sexes are mixed; and when there are more organic molecules of the male than of the female, in such a mixture the produce will be

order.' The animal spirit, carried in a germ of the 'first order,' is there fashioned again exceedingly small by the secreting organs of that organized corpuscule. The portion of the animal spirit that these organs have prepared is carried by the nerves of the germ to its ovaries and is introduced into the most developed germs or into those that I shall name the 'second order.' These germs extract again from the animal spirit the more subtle particles which pass to the germs of the 'third order' and thus the spirit passes successively into all the germs of the series, from the germ which contributes to the actual generation, up to that one which will be said to be fertile only at the end of the World."

a male; and, on the contrary, when there is more of the female than a female will be the result. . . .

I conceive, that in the aliments we take there is a great quantity of organic molecules, which needs no serious proof, since we live on animals and vegetables, which are organized substances. In the stomach and intestines a separation is made of the gross parts, which are thrown off by the excretories. The chyle, which is the purest part of the aliment, enters into the lacteal vessels, and from thence is transported into every part of the body. By the motion of the circulation it purifies itself from all inorganic molecules, which are thrown off by secretion and transpiration; but the organic particles remain, because they are analogous to the blood, and that from thence there is a power of affinity which retains them afterwards; for as the whole mass of blood passes many times through the body, I apprehend, that in this continual circulation every particular part of the body attracts parts most analogous to it, without interrupting the course of the others. In this manner every part is expanded and nourished, not, as it is commonly said, by a simple addition of the parts, and a superficial increase, but by an intimate penetration of substance, produced by a power which acts on every point of the mass; and when the parts of the body are at a certain growth, they are almost filled with these analogous particles, as their substance is become more solid. I conceive that they then lose the faculty of attracting or receiving those particles, but as the circulation will continue to carry them to every part of the body, which not being any longer able to admit them as before, must necessarily be deposited in some particular part, as in the testicles or seminal vessels. This fluid extract of the male, when mixed with that of the female, the similar particles, possessing a penetrating force, unite and form a small organized body like one of the two sexes, and no more than expansion is wanting to render it a similar individual, which it afterwards receives in the womb of the female.

In commenting on Buffon's views, Darwin stated, "If Buffon had assumed that his organic molecules had been formed by each separate unit throughout the body, his view and mine would have been very closely similar." It is interesting for us to note that as late as 1883 William Keith Brooks accepted the hypotheses of both Darwin and Buffon. From his "The Laws of Heredity," p. 85:

The mode of origin and transmission of the gemmules is essentially like Darwin's conception, and we must acknowledge that Buffon's view of the part played by his organic molecules was very near the truth.

The hypothesis of pangenesis is, of course, far older than the work of Spencer, Bonnet or Buffon. Indeed, it is found, fully developed, in the very earliest scientific

contributions of the Greeks, in the works of Hippocrates and Democritus. Aristotle examined the doctrine carefully and discarded it, but four hundred years later, at the time of Galen, it had become firmly imbedded in medical literature. It was accepted by the early church fathers, the medieval scholars and the naturalists of the sixteenth and seventeenth centuries. Attention has frequently been called to the fact that Hippocrates, Democritus and Aristotle knew of pangenesis,⁶ but the biologists of to-day do not seem to have realized how completely and exactly the ancient philosophers visualized the problem or how clearly they discussed the principles involved. Ernst Haeckel's somewhat superficial judgment has been widely accepted. In "The History of Creation" (Vol. I, p. 78—Ed. of New York, 1896) he stated, "We have therefore no special occasion to examine the natural theories of development of the various Greek philosophers, since they were wanting in the knowledge gained by experience, both of organic and inorganic nature."

This statement of Haeckel's is little more than a justification for intellectual inertia. Its essential superficiality is shown by the fact that it contains a tacit assumption that Haeckel's own theories of development, and those of his contemporaries, were founded upon knowledge gained by experience. Haeckel was a convinced Lamarckian and the inventor of the biogenetic law.

If we were to search the works of Hippocrates for a statement of the pangenesis hypothesis we would naturally look first in his book "On Generation." There, in the very beginning (Number 1, 3), it is stated that the sperm comes from the whole body. These passages illustrate exceptionally well how little the ancients knew of anatomy:

⁶By Brock (1888), Thompson (1889), Osborn (1894), May (1917), Stiebitz (1930) and Krumbiegel (1933) among others. To the best of my knowledge, however, no complete collection of the pertinent excerpts has ever appeared in English. The medieval discussions seem to have been missed entirely.

1. Law governs everything. The sperme of man comes from all the humors which are in the body, and it is the most active part which separates off. Here is the proof: after coition, the evacuation of such a small quantity of semen renders us feeble. The disposal is thus: veins and nerves run from the whole body to the genital parts; rubbed, warmed, and full, a longing occurs which gives pleasure and warmth to the whole body. The humors grow warm in the body with the friction of the genitals and their movement. They dilate and are stirred by the movement, and become frothy just as all liquids become frothy when agitated. In this manner, in man, the sperm separates itself, the humor becomes frothy, the most active and most corpulent part collects in the dorsal marrow; in effect it collects there from the whole body, the brain particularly discharges into the loins, and into the marrow, which, in its turn, is supplied with efferent veins in order that the humor may both flow there, and later leave. The sperm, once it has arrived in the marrow, passes along the kidney; for that is where the channel is through the veins; and in case of ulceration of the kidneys, evacuated with the semen. From the kidneys, the semen proceeds to the thousands of parts of the testicles and to the genital member, not by the urinal tract but by an other particular tract (ejaculatory ducts) which is close by.

3. I say that the sperm comes from the whole body, from the solid parts as well as from the soft parts and from all the humors which are in the body.

Hippocrates comes much closer to pangenesis in a brief statement in the book known as "The Sacred Disease":

As the seed comes from all parts of the body, healthy particles will come from healthy parts, and unhealthy from unhealthy.

A still better description of pangenesis occurs in a short paragraph in "Airs, Waters, Places" (XIV). Here Hippocrates states the essential presuppositions upon which the hypothesis of pangenesis is based, and he uses the hypothesis to explain how acquired characters could be inherited. The following passage shows how completely Darwin was forestalled in 400 B.C.

... I will begin with the Longheads. There is no other race at all with heads like theirs. Originally custom was chiefly responsible for the length of the head, but now custom is reinforced by nature. Those that have the longest heads they consider the noblest, and their custom is as follows. As soon as a child is born they remodel its head with their hands, while it is still soft and the body tender, and force it to increase in length by applying bandages and suitable appliances, which spoil the roundness of the head and increase its length. Custom originally so acted that through force such a nature came into being; but as time went on the process became natural,

so that custom no longer exercised compulsion. For the seed comes from all parts of the body, healthy seed from healthy parts, diseased seed from diseased parts. If, therefore, bald parents for the most part bald children, grey-eyed parents grey-eyed children, squinting parents squinting children, and so on with other physical peculiarities, what prevents a longheaded parent having a long-headed child? At the present time long-headedness is less common than it was, for owing to intercourse with other men the custom is less prevalent.

Hippocrates' doctrine of the inheritance of acquired characters and of the mechanism which transmitted them is really the same as Darwin's. The slight differences between the two are apt to be magnified, however, by our reading our own twentieth century conceptions into Darwin's work. Darwin never pictured his gemmules as hormones or other organic compounds which merely collected in a germ-plasm which was itself continuous from one generation to another. The gemmules were supposedly the primordia of cells. Then too, Darwin's conception of the rôle of the semen in fertilization was very crude. He considered very carefully the theory that the foetus was developed from an egg impregnated by a single spermatozoan and he discarded it entirely, for he believed that the whole semen was the fecundating substance and that the foetus would resemble the father or the mother in proportion to the amount of material each contributed to its formation. Thus he supposed that a large discharge of semen tended to make the resulting child resemble its father. Moreover, Darwin went so far as to accept telegony, and he even thought that the female herself was altered specifically by the semen she received from the male ("Animals and Plants under Domestication," Ch. XI), as gemmules supposedly could migrate from the germ-plasm into the body as well as in the reverse direction.

Democritus' description of pangenesis was in a work which has been lost, but we know of his contribution through a short passage quoted by Plutarch. This is included in the collection of Plutarch's works known as

the "Morals." The work in question is "De placitis philosophorum." From Book V, Chapter 3:

Democritus (says) that it (semen) proceeds from all parts of the body, and chiefly from the principal parts, as the flesh and muscles.

On the other hand, Aristotle utterly rejected pangenesis, after considering it seriously and arguing the matter pro and con in the approved *a priori* manner of his time ("De gen. animal.," I: 17, I: 18). In favor of pangenesis he urged (1) the intense pleasure of coition, pleasure felt by the whole body; (2) the alleged inheritance of mutilations; (3) the resemblance of young to their parents, part for part; and (4) the reasonableness of the supposition that, as the whole arises from some primordium (the semen), each part should have a seed peculiar to itself. The arguments against pangenesis seemed the stronger, however, and he rejected the doctrine. He held that the resemblance of children to their parents was no proof of pangenesis, for they resembled their parents in hair, nails, voice, movements, etc., which of course could produce no gemmules. He also gave many additional reasons for rejecting the doctrine, but as they are practically meaningless, they need not be repeated here.

In spite of Aristotle's opposition the belief in pangenesis continued to flourish, particularly in medical literature. It is definitely indorsed in "An animal sit id, quod in utero est," a book which has generally been ascribed, though probably falsely, to Galen (130-200 A.D.) From chapter 2:

When a child is in the uterus, it should show the behavior of an animal, just as Hippocrates of the tribe of the Asclepiades says . . . ; for he sets up as his first definition the derivation of the animal from the whole body since he does not see how otherwise it would be able to appear complete unless he could believe that the animal is generated by the whole. He says, "The seed comes from every part of the body, the healthy from the healthy, but the diseased from the diseased." He said that from the sum of all the parts, the whole was produced: (and he was wrong only in calling the foetus an animal, so that he disparaged the judgment of those who said the

opposite; namely that those things which were mutilated have not been perfected or completed). For since he was unwilling to doubt that it was an animal, he said indeed that healthy bodies place aside a perfect seed, whole in this way, namely, that they lack nothing in substance: but bodies which are impaired place aside a seed with a defect. . . . Rightly therefore, according to Hippocrates, will that animal which is in the womb be said to be fertile in that it is produced from the whole and is offered the strength of the whole. But, he not only declared that the animal is derived from the very whole, but he also showed that the primordia have the same potentialities as the whole of those from whom it has taken its roots. . . .

The early fathers of the Christian Church likewise had occasion to discuss the origin of semen. The theological problems of original sin and the second birth could often be explained more easily to the Pagans if similes from natural history⁷ were used. Consequently many works of religious propaganda contain unexpected records of the current biological beliefs. While opinion concerning the nature and the point of origin of the semen was far from unanimous, the majority of the writers seemed to favor the view that it was produced from the whole body.

Clement of Alexandria, who probably wrote most of his books between 193 and 211 A.D., suggested indirectly in the "Instructor" (Book II, Chapter XI) that the seed was produced from the whole body, although the passage in Genesis which he quoted refers to the production of Eve from Adam's rib. He stated:

For he says, "Now this is bone of my bones and flesh of my flesh." Therefore man is drained of seed as is shown by the body, for that which is produced (by the body) is the beginning of generation; nay, merely the bubbling out of material confounds, weakens and agitates the structure of the body.

Lactantius (260-340 A.D.) evidently considered the question but could come to no decision. From "The Workmanship of God," Chapter XII:

But that the right part contains the masculine seed, the left part the feminine; and altogether, in the whole body, the right part is masculine but the left feminine. Certain ones think that the seed itself comes only from

⁷ St. Augustine, "Marriage and Concupiscence," I: 21, I: 37, etc.

the medulla, and certain ones think that the seed flows to the genital vein from the whole body.

St. Isidore of Seville indorsed the Hippocratic theory of the origin of the sperm. He wrote "Etymologiarum" some time between 622 and 633 A.D. From Book XI, No. 1:

A seed is that which, having been cast off, is taken up either by the earth or by the uterus for producing either fruit or foetus. For there is a liquid, formed from a mixture of the food and the body which diffused through the veins and medulla and exuded as refuse, takes form in the kidneys, and, having been ejected through coitus and received into the uterus, is formed in the body by a certain heat of the internal organs and by the irrigating of the menstrual blood.

The encyclopedists of the remarkable thirteenth century seemed to have been almost as interested in the origin of the sperm as were the biologists of the nineteenth. Bartholomew the Englishman (Bartholomaeus Anglicus), who wrote between 1230 and 1240, indorsed pangenesis. The following excerpt is taken from the translation of John Trevisa printed at Westminster in 1495. Bartholomew's work was translated as "All the propyrties of thynges." From Book VI, Chapter III:

The matere of ye chyld is matere seminalis, that is shedde by werkynge of generacōn/ And comyth of all ye partyes of the fader & the moder/ fyrste this matere is shedde in ye place of conceyvyng abroad. that is by the drawynge of vertue of kynde heete/ for if the degeste blood of the fader & moder were not medlyd togyder, there myghte be noo creacōn nother shapynge of a childe. For the matere of blood ye comyth of the male is hote & thycke/ And therefore for the grete thykenesse it maye not sprede itself abroad.

Vincent of Beauvais, following Aristotle, denied pangenesis ("Speculum naturalis" Book XXIII, Chapter 35, 1244-1254 A.D.), but St. Albert the Great was convinced that the semen was produced by the entire body and he described its production both in "De Animalibus" and "De Nutrimeto," written probably around 1254-1256 A.D. From "De Animalibus," Book 3: Tract 2: Chapter 8: No. 15:

Hippocrates of Cos said, however, that all sperm descends from the head through two veins which he calls spermatica. They are continued behind the ears in the nape of the neck where the upper part of the neck joins the head and finally they lead to the kidneys and therefore pleasure is also felt in the kidneys. At last they come to the genitalia, and he says there is proof of this in that certain ones having been wounded in war even to the breaking off of these veins suffer sterility and can no longer produce sperm. Galen said however that he didn't know whether what Hippocrates says was true or not: but he said *à propos* of this idea that it was more probable that the sperm, which was the "superfluous" of the fourth digestion, exudes from all members of the body but especially from the head and receives by chance a mixture in the head for it is completed there more quickly, because in the head are the more noble forces of the soul. However, the "porousness" of similar members, the semen is lowered and is attracted by the testicles, just as blood is drawn by "ventosa," and in the testicle it is whitened and receives a further refining the virtue of which comes from the heart, and then it is complete for generation, just as we said in the other (cases). There is proof that it exudes from all members of the body because it has the potentiality of forming the whole body: and we see in many animals a member lacking at birth which was deficient in the generating forces. Aristotle seems to believe that women may not have sperm and I think this is true; but this will be discussed in the following.

In the following extract from "De Nutrimeto," St. Albert definitely anticipated de Buffon. From Book I: Tract 2: Chapter 2:

Therefore as a result of these demonstrations it seems that the seed is taken from nourishment which is sufficiently expanded by the soul. That which is not sufficiently assimilated, however, is not sufficiently dispersed. And therefore it is necessary that there be a cutting off of the seed by the final digestion of nutriment before it is united to the body. This occurs, however, when the fourth digestion has been completed in itself. And therefore Aristotelian philosophers say that the seed is the superfluity of food (left) after the fourth digestion and taken from the whole body and particularly from the head: indeed from the whole body because it is entire in potentiality and because it can produce every member. However, it comes down more from the head than from any other single member; on account of this, namely, the fact that the soul houses itself in it not as the first impulse of the body, but as an artificer fashioning for himself a dwelling place. And because the properties which separate the animate from the inanimate, that is, movement and sense, are in the head, and therefore it comes down particularly from the head. Moreover, a proof of this is the fact that workings of the brain are greatly weakened by much coition: and a further proof is that if certain veins next to the temples, which are called spermatical, are broken, no more sperm is produced.

Moreover, the seed having been thus released from the whole body as Constantine says, it follows two special veins through which it descends to

the testicles, which two veins opened through the heat caused by the friction of coition emit the seed in coition. This indeed is not probable. For, since it is necessary for the seed to be cut off from the whole body, it is necessary for these two veins to terminate at all the members. Moreover, up to now, since the start of the veins is from the heart or from the liver, it is fitting that first there be an overflowing and the seed ought to distill to the seminal vessels, which indeed does not seem probable as is shown by experiments. And therefore this is more probable that the seed diffuses through the "porousness" of the body and is drawn by the testicles just as "atrahit ventosa," and just as nutriment is carried to the members, as Aristotle said. The temperature of the body having been excited by coition; and the pores are opened so that the seed descends, which when it has descended, receives the formative virtue in the testicles, which virtue is present in these testicles, and this formative virtue is in the heat and the substance of the seed and is retained in the sperm through the very viscosity of the sperm. Moreover, this formative virtue is called "the life of the sperm": for the reason that it has the same principle as the soul.

No treatment of the pangenesis hypothesis could be adequate which left out the work of St. Thomas Aquinas. St. Thomas referred to the problem several times in his "Summa Theologicum," but his real contribution is a 4,000-word essay in the second book of his "Commentum in quatuor libros sentiarum magistri Petri Lombardi." The essay is in Dist. XXX; Quaest. II; Art. II, and bears the title "Utrum semen decidatur ex eo quod generatur ex alimento." No short selection from this work could do the author justice, for the essay should be viewed as a whole. St. Thomas examined carefully and skeptically the earlier theories in the light of his own thirteenth century knowledge and weighed very logically what evidence he had. It is true that he sought to find in the semen both a physical basis for the transmission of original sin and a biological justification for a belief in the bodily resurrection, but the greater part of the article is restrained and scientific. He preceded Darwin by just a little over six hundred years. He also forestalled Buffon as he traced the ultimate origin of the gemmules to the organic particles assimilated as food. Indeed the eighteenth and nineteenth century naturalists would appear in a very different perspective if the thirteenth century contributions were more available or better known.

In even a cursory search for possible descriptions of pangenesis the writings of Peter of Crescentius would be among those examined. In 1305, Peter wrote his "*Opus ruralium commodorum*," a work which remained so popular that more than forty-five printed editions were issued in six different languages before the middle of the seventeenth century. Thirteen of these editions are incunabula. Unfortunately, many of the later issues were brought up to date by very careless editors and translators and the order of the books and the arrangement of the chapters were often scrambled. Since few, if any, editions were indexed properly, collation is not easy.

Pangenesis is described in a German edition issued as "*New feldt undt ackerbaw*," Strassburg, 1602. This description can not be ascribed to Peter himself, as it seems to be lacking in many of the earlier editions.⁸ The following passage is taken from Book III; Chapter 8; page 166:

The naturalists now state that the seed does not come from one or two parts of the body, because it should then happen that only such parts would grow from the seed as those from which the seed came, and the creatures would not be the same as those created and governed by God. One must admit this not only among human beings but also among the irrational animals, for they are born (monsters and mis-births excepted) with the measure of all the parts of their entire bodies the same as their parents, except that they are small as are all new born creatures, which have not yet grown, and it must necessarily follow that the seed must come out of the whole body, that is out of all the members of the body.

George Valla (d. 1500) presented several different theories of the origin of the semen, but did not choose between them. From "*De rebus expetendis et fugiendis*," Venetiis, 1501, Book XXI, Chapter 76:

WHAT THE ESSENTIALS OF THE SEED ARE

Aristotle says that the seed is that which is able to form from itself and produce something of the same kind, as that from which it had been created. Pythagoras says that the fourth of the most useful blood is the seed, the

⁸ The writer was able to examine five other editions but could find nothing which corresponded to this passage. These were (Latin) Argentinæ, 1486; (Italian) Vicenza, 1490; Venetia, 1542, 1553, 1564.

excess of the food, as the blood and the medulla. Alemaeon says it is a part of the brain. Plato says it is the discharge of the moist medulla. Epicurus says it is the tearing off of the soul and the body. Democritus says that the seed is from the whole body and from the most potent parts of the fleshy nerves which certain ones call hairy, other Greeks call them little veins consisting of threads.

Franciscus Marius Grapaldus in "De Partibus Aedium," Parma, 1506 (fol. 86), preferred to accept the medulla as the place where the sperm was formed, but Rhodiginus, his slightly younger contemporary, stated that the semen came from the whole body in "Sicuti Antiquarum Lectionem," Venetiis, 1516. From Book XV, Chapter 23:

After that, the seed is located within the special place for forming a man, which seed has flowed down from the whole body of the man, which (view) I notice is pleasing to the most learned of the school of Plato, and this seed had dragged with it the formative force from the spirit of man. Its potentiality is such that in almost forty-five days on the first six days following milk is produced. A generative shell having been thrown around the foetus from a very thin membrane such as in an egg, it becomes enclosed by the outer skin: this is understood by doctors, nor did Hippocrates keep silent concerning it in his book "Concerning the Nature of a Child."

Slightly later Paracelsus also stated that the semen came from all the members of the body, and he described its production in several of his many works written in the second quarter of the century. Perhaps the most complete description is in "De generatione Hominis." Haartmann quoted a very pertinent excerpt in his "Paracelsus" (London, 1887). From page 63:

From this nerve-aura or liquor vitae, in the process of the generation of man, the *semen* separates itself in a manner comparable to the separation of the foam or froth from a fermenting liquid, or as the quintessence (the fifth principle) of all things separates itself from the lower elements. This semen, however, is not the sperma or the visible seminal fluid of man, but rather a semi-material principle contained in the sperma, or the *aura seminalis*, to which the sperma serves as a vehicle. The physical sperma is a secretion of the physical organs, but the *aura seminalis* is a product (or emanation) of the "liquor vitae." It is developed by the latter in the same sense as fire is produced out of wood, in which there is actually no

⁹ This passage is in Volume II, page 289 of his "Opera Omnia," Genevae, 1668.

fire, but out of which heat and fire may proceed. This emanation or separation takes place by a kind of digestion, and by means of an interior heat, which during the time of virility may be produced in man by the proximity of woman, by his thoughts of her, or by his contact with her, in the same manner as a piece of wood exposed to the concentrated rays of the sun may be made to burn. All the organs of the human system, and all their powers and activities, contribute alike to the formation of the semen; and the essences of all are contained in the *liquor vitae*, whose quintessence is the *aura seminalis*, and these organs and physiological activities are reproduced in the foetus out of this liquor. They are therefore germinally contained in the seminal fluid that is necessary for the reproduction of the human organism. The semen is, so to say, the essence of the human body, containing all the organs of the latter in an ideal form.

The great mathematician and physician, Jerome Cardan (1501-1576), also concluded that the semen was derived from the whole body. The following passage is from his "*Contradicentum Medicorum*," Book II: Tract VI; *Contradict.* XVII. In his "*Opera Omnia*," Lugduni, 1663, it is on pages 641-642 of volume VI:

This having been seen, we ask whether the seed is cut off from the whole body? Hippocrates in the book concerning the semen says that in the beginning the veins, arteries and nerves from the whole body extend into the private parts and therefore, the most fertile liquid which is in the whole body, comes first to the kidneys and then to the testicles until it is emitted into the vagina in coition and for this whole reason, the whole body experiences delight and in the end of the little book he says in the section concerning mutilations that the weak part which pertains to the mutilated members is spread abroad, and because of this it happens that sometimes whole children are produced and sometimes mutilated children are born from mutilated parents. Aristotle also in the fourth book of *Problems* asks why buttocks and eyes particularly suffer in sexual indulgence, and he answers in reply that the eyes are distended because either the seed itself or something in it is sent out from the brain and thus he thinks that the seed is taken from the brain and from other parts, since this more clearly marks out the reason why sexual indulgence delights so much. For he says that the seed either is cut off from the whole body as certain of the ancients thought, or at least the veins from the whole body and all the avenues of sensations in the body extend into that part from which it comes. He firmly declares this when he shows why a man is particularly weak from intercourse, he says because the seed comes from the whole body, otherwise, it would be necessary that some parts suffer nothing at all which is a view opposed to experimental evidence. Avicenna also has these views: and it seems to me that the seed is not from the brain alone, but the source of this seed is from every principal member and it even exudes from other parts, nor is the whole seed from the brain itself although it is prepared in the brain, and although he seems to assign to Hippocrates what he

thought, namely that the seed is cut off only from the brain, he did not dare to announce this. And rightly, for Hippocrates (since the authority produced above seems to be from the Greek writing of Polybius) in his book concerning Air and Water says, while he is writing concerning the people of Pontus, that the seed comes from all parts of the body, and therefore bald children arise from the bald. In the second book concerning the Generation of animals, the Philosopher says that the seed itself contains in potentiality all parts of the body and is set in motion by that force by which the whole body is enlarged. Besides the two reasonings deduced from Hippocrates we bring others, for, as is shown, the whole body of an animal is injured by castration, and this would not occur unless the testicles could not longer carry the strength into the whole body; however, there is no strength unless there is a drawing together of the seed, for the seed is blended with the nourishment of the members when it is drawn off, and it transforms and injures all the members themselves (when it is drawn off), therefore it must necessarily be derived from the whole body. Again, it is necessary that everything which is such in potentiality be from something which actually is such in fact.

The Dutch physician, Levinus Lemnius, used the pangenesis hypothesis to explain the heritability of disease. From "*Occulta naturae miracula*," Antwerpiae, 1561, Book I, Chapter 4:

Seeing that the seed flows from the principal parts, and contains in it the force and nature of all the members, it comes to pass that what disease is in any part, descends by right of succession to the children.

Book I, Chapter 9:

Wherefore there are two things especially that perfect copulation, and that help to beget Children: First, the genital humour which proceeds partly from the brain and the whole body, and partly from the Liver, the fountain of blood. Then the Spirit that comes by Arteries from the Heart, by force whereof the yard is erected, and grows stiff, and by the force whereof the seed is ejected. . . .

Nicolas Venette indorsed pangenesis in his discussion of animal hybridization and the production of monsters. From "*La generacion de l'homme on tableau de l'amour conjugal*," Amsterdam, 1687, page 538:

It is therefore easy to recognize the cause of monsters, without giving myself the trouble of pointing it out; because if it is true, as I have proved elsewhere that the seed is given life and that it comes from all parts of the body of the two sexes as experience shows us, it seems to me that it is no longer necessary to discover the immediate cause of the inclinations and of the form of the body of monsters.

John Ray first published "The Wisdom of God Manifested in the Works of Creation" in 1691. Like many of his predecessors he used the hypothesis of pangenesis to explain the hereditary transmission of characters:

Yet it must be confessed that the Seed of Animals is admirably qualified to be fashion'd and form'd by the *Plastick Nature* into an organical Body, containing the Principles or component particles of all the several homogeneous Parts thereof; for indeed every part of the Body seems to Club and contribute to the Seed, else why should parents that are born blind or deaf or that want a finger or any other Part, or have one superfluous, sometimes generate Children that have the same Defects or Imperfections? . . .

With Peter Louis Moreau de Maupertius we return to the eighteenth century and to contemporaries of Bonnet and Buffon. Maupertius endorsed pangenesis in his "Système de la Nature." The following passages are from his collected work, "Oeuvres," Lyon, 1756 (Vol. II, pages 159-164):

XXXIII

The elements adapted to form the foetus float in the seeds of the father and mother animals: each extract of the part, similar to that which it is to form, maintains a kind of souvenir of its original condition; and it will tend to take it back again whenever it is able to form the same part in the foetus.

XXXIV

Hence, in ordinary order, the conservation of the species and the resemblance to the parents.

XXXV

If some elements are lacking in the seeds where they are not able to unite, there are born monsters in whom some part is lacking.

XXXVI

If the elements occur in too great a quantity or if after their visual union, some part remains uncombined it may unite itself to some other part and there is born a monster with superfluous parts.

XXXVII

Certain monstrosities, perhaps by excess, perhaps by defect, perpetuate themselves ordinarily enough from one generation to another, or even through several generations. One knows of a family in Berlin where commonly the children were born with six fingers, which is transmitted as much by the father as by the mother. This phenomenon of which one will find several examples if one hunts them, is inexplicable in either one or the other of the two systems on generation now universally accepted; or

rather it reverses absolutely both of these systems, the one which supposes the child formed entirely within the father, and the one which supposes the child formed entirely in the egg of the mother before the copulation of the two sexes: because if either one or the other of the systems is true, if we shall have observed numbers of generations of six-fingered individuals, each generation contained in the preceding, the monstrosity would have to be heritable only through the father (according to the first system) or only through the mother (according to the second system). In our case, there is not any difficulty: the first monstrosity having been the accidental effect of some of the causes described in the preceding paragraph, the habit from the situation of the parts in the first individual, makes them replace themselves in the same manner in the second, in the third, etc., as long as that habit is not destroyed by something else more powerful, maybe on the part of the father, or on the part of the mother, or by something accidental.

This brief survey of the descriptions of pangenesis may very well end with a quotation from von Haller. It is taken from his "*Elementa Physiologie*," Lausanne, 1778.

The head contains germs of the tail and the tail germs of the head, so that when one is cut off, the other furnishes a supply of germs and these consequently receiving more nutriment are developed.

SUMMARY

1. Lamarck was neither the first nor the most distinguished biologist to believe in the inheritance of acquired characters. He merely endorsed a belief which had been generally accepted for at least 2,200 years before his time and used it to explain how evolution could have taken place. The inheritance of acquired characters had been accepted previously by Hippocrates, Aristotle, Galen (?), Roger Bacon, Jerome Cardan, Levinus Lemnius, John Ray, Michael Adanson, Jo. Fried. Blumenbach and Erasmus Darwin among others.

2. If we wish to trace the history of evolution, we should search for naturalists who lived before Lamarck and who did not believe in the inheritance of acquired characters. Brock listed but two, (1) the unknown editor of Aristotle's "*Historia Animalium*," and (2) the philosopher, Immanuel Kant.

3. The dogma of the immutability of species met with general acceptance only late in the eighteenth and early

in the nineteenth century. Botanists from the time of Theophrastos to the time of Linnaeus believed in "degeneration." "Degeneration" did not then have its modern meaning, but was synonymous with De Vriesian mutation. Belief in degeneration was not incompatible with belief in special creation, as its effects were supposed to be neither orderly nor cumulative.

4. In order to understand what Charles Darwin meant by his provisional hypothesis of pangenesis, it is necessary that we do not give to the terms he used the meanings which they acquired during the twentieth century. Darwin's conception of the germ-plasm was not the one currently accepted. He considered the theory that the foetus was produced from an egg fertilized by a single spermatozoan but rejected it. He believed that the whole semen was a fertilizing substance and that the foetus resembled the father in proportion to the amount of semen ejaculated in coition. Furthermore, he believed in telephony and in the specific influence of semen upon the mother's body.

5. The hypothesis of pangenesis is as old as the belief in the inheritance of acquired characters. It was endorsed by Hippocrates, Democritus, Galen(?), Clement of Alexandria, Lactantius, St. Isidore of Seville, Bartholomeus Anglicus, St. Albert the Great, St. Thomas of Aquinas, Peter of Crescentius (?), Paracelsus, Jerome Cardan, Levinus Lemnius, Venette, John Ray, Buffon, Bonnet, Maupertius, von Haller and Herbert Spencer. A careful search of our available records should add a number of names to this list.

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THE SHELTERING OF LETHALS

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FROM the time of Müller's brilliant demonstration of balanced systems of lethal factors, a number of writers have taken the view that enforced heterozygosis by itself is sufficient to explain the accumulation of lethals in the sheltered chromosome. Thus it has been proposed that the genetic inertness of the Y-chromosome in *Drosophila* has arisen by the gradual accumulation of mutations having an inactivating effect on portions of this chromosome, it being supposed that such mutations would be sheltered by the mechanism of sex-linkage from the counter-selection by which mutations of this kind would, in other cases, be kept in check. The finding in *Drosophila* of a corresponding inert region in the X-chromosome is clearly at variance with this view, as also is the possibility of obtaining homozygotes for factors such as those producing the short-style in heterostyled plants, which are maintained constantly heterozygous, so long as only legitimate fertilizations are used, and which would therefore be expected to be accompanied by closely linked lethals. The following investigation shows that, by itself, enforced heterozygosis gives no such shelter to lethal mutations as would explain their accumulation from this cause alone.

Consider an animal or a plant invariably propagated by the union of members of two classes, one heterozygous, Aa, for a determinate factor, while the other is homozygous, aa. The chromosomes bearing the genes A and a will be supposed initially to be, in other respects, similar. The introduction of a lethal mutation in the same chromosome makes possible three types of organisms of the heterozygous class, namely AL/aL , Al/aL and AL/al , which we shall suppose to occur in the population with frequencies u , v , w , where

$$u + v + w = P.$$

In the homozygous class there are, in addition, two possible types aL/aL and aL/al , which we shall suppose to occur with frequencies x and y , where

$$x + y = Q,$$

and

$$P + Q = 1.$$

The presence of the lethal in the population will be supposed to be maintained by a mutation rate, μ , affecting all gametes bearing L . Homozygotes ll are, of course, inviable. The relative frequencies of the possible types of gamete, taking account of the incidence of mutation, from these five types of organism may best be shown in Table 1.

TABLE 1
TYPE OF GAMETE

Parent organism	AL	Al	aL	al
AL/aL	$u(1-\mu)$	$u\mu$	$u(1-\mu)$	$u\mu$
Al/aL	—	v	$v(1-\mu)$	$v\mu$
AL/al	$w(1-\mu)$	$w\mu$	—	w
aL/aL	—	—	$2x(1-\mu)$	$2x\mu$
aL/al	—	—	$y(1-\mu)$	$y(1+\mu)$

It will be noticed that the entries in the first three lines of the table have a total $2P$, while those in the last two lines have a total $2Q$; but these factors will not require separate consideration.

Any condition of equilibrium of the system may be recognized by making the frequencies of the zygotic types proportional to products of the gametic types which produce them. If this is so we shall have the equations:

- (1) $ku = (u + w)(2x + y)(1 - \mu)^2$
- (2) $$
- (3) $kw = (u + w)\{ 2x\mu + y(1 + \mu) \} (1 - \mu)$
- (4) $kx = (u + v)(2x + y)(1 - \mu)^2$
- (5) $ky = (2x + y)\{ (u + v)\mu + w \} (1 - \mu)$
 $\quad + (u + v)\{ (2x + y)\mu + y \} (1 - \mu).$

In order to take account of all possibilities the steps of solution will be set out formally. By addition of equations (1) and (3) it appears that

$$(6) \quad k(u + w) = 2Q(1 - \mu)(u + w),$$

whence it follows that either

$$(6a) \quad k = 2Q(1 - \mu)$$

or

$$(6b) \quad u + w = 0.$$

In the second solution, since negative frequencies are not to be considered, u and w are both zero; and, in fact, all gametes containing A also carry the lethal l . It is, no doubt, the possibility of this solution which has inclined writers who have discussed the subject to the belief that it would be brought about merely by the occurrence of lethals closely linked with the heterozygous factor. A natural population, however, would not by itself tend to this condition unless AL gametes, supposing some of these to exist, were at a selective disadvantage, when account is taken of their mutation rate, compared with Al gametes; whereas it is manifest that unless al gametes are very rare the AL gametes would be at a selective advantage, and, if initially in a small minority, would tend to increase up to some frequency of equilibrium which must be given by the first solution, (6a).

To complete this solution we may note that from equations (1) and (2)

$$(7) \quad k(u+v) = (2x+y)(1-\mu)P,$$

whence

$$(8) \quad 2Q(u+v) = P(2x+y).$$

Also, by doubling equation (4) and adding equation (5), it appears that

$$(9) \quad \begin{aligned} k(2x+y) &= (2x+y)(1-\mu)P + 2(u+v)(1-\mu)Q \\ &= 2(2x+y)(1-\mu)P. \end{aligned}$$

Hence

$$2Q(1-\mu) = k = 2P(1-\mu),$$

so that the frequencies of the two classes of organisms represented by P and Q are equal, each being one half.

With the aid of equation (8) we may now write equation (4) in the form

$$2x = (1-\mu)(x + \frac{1}{2})^2,$$

leading to the solutions

$$x + \frac{1}{2} = \frac{1 \pm \sqrt{\mu}}{1-\mu};$$

writing

$$\mu = z^2,$$

this gives

$$x + \frac{1}{2} = \frac{1 \pm z}{1-z^2} = \frac{1}{1-z} \text{ or } \frac{1}{1+z},$$

of which the first value is greater than unity, while the second is less. Since $y = \frac{1}{2} - x$, and can not be negative, we must choose the lesser value and obtain

$$x = \frac{1-z}{2(1+z)}$$

$$y = \frac{z}{1+z}$$

and, by substitution,

$$u = \frac{1-z}{2(1+z)}$$

$$v = \frac{z}{2(1+z)}$$

$$w = \frac{z}{2(1+z)}$$

The two types of double heterozygotes having frequencies v and w are thus equally frequent, as though linkage did not exist, while heterozygotes for the lethal are equally frequent in Aa and in aa organisms. The enforced heterozygosis of A has had no influence whatever on the situation in which the lethal mutant is in equilibrium.

UNEQUAL MUTATION RATES

Since the effective reason for the rarity of Al gametes, when the frequencies are in equilibrium, lies in their elimination when united with al gametes, it is instructive also to examine the consequences of postulating different mutation rates for the lethal in chromosomes carrying A and a , respectively. For simplicity we shall now write ν for $1 - \mu$ in the A -chromosome, and ν^1 in the a -chromosome. Equation (6b) is then unchanged, but in place of (7) and (8) we have

$$k(u+v) = (2x+y)P\nu^1,$$

and

$$2Q\nu(u+v) = P\nu^1(2x+y).$$

Further it appears that

$$k(2x+y) = (2x+y)P\nu^1 + 2(u+v)Q\nu^1,$$

which is now equivalent to

$$(2x+y)P \frac{v^1(v+v^1)}{v};$$

so that

$$\frac{P}{2v^2} = \frac{Q}{v^1(v+v^1)} = \frac{1}{2v^2 + vv^1 + v^{12}}$$

The two complementary classes of organisms are in this case nearly, but not exactly, equally frequent. Substituting in equation (1), it now appears that

$$2(v+v^1)^2x = v^1(2v^2 + vv^1 + v^{12})(x+Q)^2.$$

If the roots of this quadratic are real, one will be greater than Q , and therefore unacceptable, while the other is less, as in the previous case; but they are only real when the quantity

$$v + v^1 - 2v^{12}$$

is positive. This will always be the case when v is equal to or greater than v^1 , or when mutation is less active in a chromosome containing A than in one containing a ; but, in the opposite case, it is possible for there to be no real solution.

In place of the expression,

$$v + v^1 - 2v^{12},$$

we may write

$$2\mu^1(2 - \mu^1) - \mu - \mu^1,$$

or

$$3\mu^1 - 2\mu^{12} - \mu.$$

Since μ^{12} will generally be very small compared with μ^1 , the condition for the unreality of the equilibrium value may with a good approximation be stated in the form that μ shall equal or exceed $3\mu^1$, or that the mutation rate in chromosomes carrying A shall be three times as great as that in chromosomes carrying a . The severity of this requirement would fully explain why it is that lethals do not appear, in fact, to have accumulated in many known cases of enforced heterozygosis.

THE STABILITY OF THE SOLUTION WITH FIVE GENOTYPES

The algebraic reality of the solution with five genotypes is not, however, a sufficient condition for its stability. Whenever two solutions of the conditions of equilibrium exist, we may be sure that if one is stable, the other is unstable, and *vice versa*. Consequently, it will be sufficient to examine the stability of the solution

with three genotypes in which u and w are both zero. The fundamental equations for this solution are

$$kv = v(2x + y)(1 - \mu^1)$$

$$kx = v(2x + y)(1 - \mu^1)^2$$

$$ky = (2x + y)v\mu^1(1 - \mu^1) + v\{(2x + y)\mu^1 + y\}(1 - \mu^1)$$

whence, since v can not be zero,

$$k = (2x + y)v^1,$$

$$x = v\mu^1,$$

or, eliminating v and k ,

$$y(2x + y)v^1 = 2(2x + y)x\mu^1 + xy,$$

or

$$v^1 y^2 + \{2x(v^1 - \mu^1) - x\}y - 4x^2\mu^1 = 0.$$

In the solution,

$$\frac{y}{x} = \frac{-1 + 4\mu^1 + \sqrt{1 + 8\mu^1}}{2(1 - \mu^1)}$$

we may with advantage put

$$(1 + 4z)^2 = 1 + 8\mu^1,$$

or,

$$\mu^1 = z(1 + 2z).$$

Then we find

$$\frac{y}{x} = \frac{4(1 + z)z}{(1 - 2z)(1 + z)} = \frac{4z}{1 - 2z},$$

and so,

$$\frac{y}{2(x + y)} = \frac{2z}{1 + 2z}.$$

Now the proportion of the gametes from aa organisms which carry the lethal is

$$\frac{y + \mu^1(2x + y)}{2(x + y)} = \frac{2z + \mu^1}{1 + 2z} = \frac{z(3 + 2z)}{1 + 2z}.$$

This must be the proportion of Al gametes eliminated in each generation. If now a sprinkling of AL chromosomes were introduced, they would suffer no elimination through lethality, but would be diminished only by mutations of L to l at the rate μ in each generation.

Consequently, unless the rate of mutation from L to l in the presence of A satisfies the relation

$$\mu \geq \frac{z(3+2z)}{1+2z},$$

the *AL* gametes will increase in proportionate numbers, or, in other words, the solution in three genotypes will be unstable. The condition for the stability of the solution in five genotypes is, thus, when μ is small, approximately that μ shall be less than $3\mu^1$. At higher mutation rates the critical ratio is somewhat nearer to equality, but does not reach equality until μ and μ^1 are each raised to unity. If μ were only twice as great as μ^1 the mutation rates would have to be raised respectively to about 36% and 18% before the stability of the solution in five genotypes would be upset.

It appears, then, that obligatory heterozygosis will only afford shelter to a lethal, or other highly disadvantageous, mutation, sufficient to allow of its establishment, in exceedingly exceptional circumstances:

(i) At ordinary mutation rates, when the mutation rate in the sheltered chromosome is almost treble that at the same locus elsewhere.

(ii) For more nearly equal mutation rates, when the rate mutation is so great that a large proportion of all the parent genes present in the species mutate in each generation.

The accumulation of lethals in such sheltered situations is therefore not likely to have occurred in natural populations.

SHELTERING BY TETRAPLOIDY

Many species exhibit recessive forms depending on duplicate or triplicate factors in which only organisms homozygous for two or more completely recessive factors are to be distinguished. It is generally believed that many of these cases originated in polyploidy. It is true that, in tetraploids of recent origin, simplex organisms, containing only one of the four possible dominant genes, are usually distinguishable from those that contain two or more, so that in these cases the typical situation of duplicate factors has not been produced by tetraploidy. However, a moderate amount of further modification in the direction of more complete recessiveness would often be sufficient to reproduce the typical case. In consequence, the effects of incomplete dominance in the simplex condition can only be regarded as evidence against the origin of duplicate factors by tetraploidy on the view, upheld by

Sewell Wright, that dominance relationships are not, in fact, modified by the selective actions available, which are, however, known to tend in that direction.

The formation of a tetraploid race, by duplicating every locus, must supply the condition for the establishment of an immense number of pairs of duplicate factors. If the tetraploid originated through hybridization of two nearly related species, the duplicated chromosomes would already be differentiated in respect of those loci which had suffered an evolutionary modification during the process by which these species had become differentiated. Unless a considerable proportion of the germinal material is usually modified by such a process, the proportion of duplicated loci must still be large. In the course of time, the number may be reduced by the extinction of the parent gene in one of the duplicate loci, and the establishment, in its place, of one of its mutant allelomorphs. It is therefore worth considering in what circumstances a lethal or otherwise deleterious gene will be able to establish itself in one of a pair of duplicate loci, under the shelter afforded by the other.

Let us suppose that inheritance is strictly diploid and that a lethal gene l appears in both loci, with mutation rate μ in each generation. Selective elimination will only take place when the double homozygotes $l_1l_1l_2l_2$ are produced. The normal genes L_1 and L_2 do not occur among the organisms eliminated; the only wastage to which their numbers are subject is that due to mutation. Consequently, the proportional frequency of both will decrease when the proportion of double homozygotes is less than μ ; both will increase when it exceeds μ ; and both will be in equilibrium when it is equal to μ , irrespective of the frequency of self-fertilization. Formally, therefore, and apart from chance fluctuations, the proportion of mutant genes in the two loci may be equal, or unequal to any extent, without upsetting the equilibrium between mutation and extinction.

DIFFERENCE OF MUTATION RATES

The fact that equilibrium is possible, whatever be the ratio of mutant genes in the two loci, shows that if the mutation rates in the two loci were different, no equilibrium would be possible, short of the extinction of the parent genes in the locus with the higher mutation rate. The rate of elimination will now lie between the two mutation rates, so that one mutant gene tends constantly to

increase, and the other to decrease. The rate of increase is thus always less than the difference between the mutation rates. The proportion of normal genes at the locus with the higher mutation rate will decrease less rapidly than the function

$$e^{-(\mu_1 - \mu_2) T},$$

where T is the number of generations. Although this supplies an under-estimate of the time required, it is correct in its order of magnitude. After a lapse of time,

$$T = \frac{4}{\mu_1 - \mu_2},$$

the parent gene will certainly be somewhat rare in the locus with the higher mutation rate. A difference of 4 per cent., in a mutation rate of one in 1,000,000, would bring this about in 100,000,000 generations. Mutation rates which were much larger and more widely unequal would of course act more quickly.

Since the opportunities for the establishment of a deleterious mutant in place of the parent gene at one of a pair of duplicate loci seem somewhat slight, attention may be given to the effects of chance at the initiation of the tetraploid form. If this originated from a single individual containing the duplicated contents of two gametes, then the race so formed would, from the first, be homozygous for any lethal factors which these gametes might contain. With cross-breeding species, a gamete chosen at random is not very infrequently the bearer of a deleterious recessive. For a lethal having a mutation rate of one in 1,000,000, the proportion of such gametes would be one in 1,000, so that this fraction of the duplicated germ-plasm may be expected to be differentiated from the start. The fraction would, however, be smaller with frequently self-fertilized organisms.

It appears, therefore, as far as deleterious mutations are concerned, that we ought to expect species which originated in tetraploidy, or members of groups of species having such an origin, to contain duplicates of almost every locus at which genetic effects can be observed. The typical appearance of duplicate factors will be conserved whenever the original parent genes have been both unchanged, or when the same gene substitution has taken place in both.

With respect to differentiation brought about by advantageous

gene substitutions, the position is, in many respects, fundamentally different. These must certainly originate with mutation rates so excessively low that their occurrence at one locus does not imply their simultaneous occurrence at the duplicate locus, even when the probability of such occurrence is strictly equal. Moreover, when, at one locus, such a favorable mutation has established itself, there is little reason to suppose that its occurrence at the second locus also will produce further advantage. Consequently, it is not improbable that such mutations will establish themselves, subsequently to the formation of the tetraploid condition, in one only of the two duplicate loci.

The differentiation of loci found in tetraploid species can, therefore, only to a minute extent be accounted for by the accumulation of lethal or deleterious mutations under the shelter afforded by the other locus. It must for the most part be due to the progressive changes which have taken place in two stages:

(a) Evolutionary differentiation by allied specific forms, prior to the formation of a tetraploid by hybridization, will have already introduced differences at a number of loci. Those who believe, with the writer, that species formation is usually accompanied by gene substitutions at a large number of different loci, each substitution having exerted, in most cases, only small morphological influence, will consider that the proportion of loci so affected may, in some cases, be large. If, on the contrary, species were formed, as some have thought, by the occurrence of only a few gene substitutions, then the vast majority of the loci in allo-tetraploids must be initially identical.

(b) Subsequently to the establishment of tetraploidy, it appears that further differentiation may proceed by progressive modifications (favorable mutations), but scarcely to any appreciable extent by regressive changes.

SHORTER ARTICLES AND DISCUSSION

RECURRENT PSEUDOMUTATION

IN connection with the behavior of the white-eared *Amaranthus* (Imai and Kanna, 1927) and of the duskish *Pharbitis*, I suggested (Imai, 1935) a theory to account for their non-heritable variation—the theory of pseudomutation, which seems to cover well the cases of mottled beans and spotted peas that I have experimented with.

The genetic nature of several types of seed-coat patterns in *Phaseolus vulgaris* was analyzed, of which the mottled character was found to be dominant to the self-colored (*cf.* Matsuura, 1933). The mottled seeds collected from a population of "Nagauzura," a stringless strain, contained 4.09 per cent. of considerably mottled or pseudo-red seeds (5,270 mottled and 225 pseudo-red). The ordinary seeds are mottled with dark-red stripes on the tinged coat (Fig. 1A), while the pseudo-red seeds are dark red



FIG. 1. Mottled (A), mosaic (B), and pseudo-red (C) beans.

with small whitish parts (Fig. 1C), the types, with the exception of a few mosaic seeds (Fig. 1B), being discontinuous in their variation. In order to investigate the hereditary behavior of the two forms, I sowed the mottled and pseudo-red seeds separately, but obtained substantially the same results, namely, non-inheritance of variation. The pseudo-red seeds gave 20 plants bearing ordinary mottled seeds, mixed together with 3.14 per cent. of pseudo-red (18 pseudo-red and 556 mottled seeds in all), while the ordinary mottled seeds produced 123 plants bearing mottled seeds mixed with 3.18 per cent. pseudo-red seeds (118 pseudo-red and 3,588 mottled seeds in all). The proportion of the pseudo-red seeds is nearly the same in the two different pedigrees. As to the occurrence of pseudo-red seeds, a pod may contain all pseudo-red seeds or a mixture of pseudo-red with mottled or mosaic seeds.

The purple-spotted form of *Pisum sativum* is a dominant character (cf. Matsuura, 1933). The spotted seeds (Fig. 2A)



FIG. 2. Spotted (A), mosaic (B), and pseudo-purple (C) peas.

are mixed together with a few pseudo-purple ones (Fig. 2C), which are self-colored but have some colorless spots (the ground color of the testa being greenish), as well as mosaic (Fig. 2B). The seeds from a population of the strain "Suzunari-Waisei-Satô" contained 20 pseudo-purple and 16,770 spotted, including some mosaics, the pseudo-purple amounting to 0.12 per cent. The two kinds of seeds were sown separately to enable an examination of their inheritance. The tests, however, showed negative results: pseudo-purple seeds gave 10 plants bearing 682 spotted seeds only, while the spotted seeds produced 249 plants bearing spotted seeds, including 0.09 per cent. pseudo-purple and 0.05 per cent. mosaic seeds (18 pseudo-purple, 10 mosaic and 21,030 spotted). The proportion of the pseudo-purple seeds is nearly constant for two generations. The manner in which the pseudo-purple and mosaic seeds appeared is as shown in Table 1.

TABLE 1

Mosaic plant No.	Spotted		Pseudo-purple (P) and mosaic (M)	
	No. pods	No. seeds	No. pods	Contents of pods
1	13	49	2	3P + 1M; 2P + 3M
2	10	43	1	2P
3	17	94	1	3M
4	38	146	1	2P + 2M
5	10	70	2	5P; 4P + 1M
Total	88	402	7	18P + 10M

The changed pods contained either all pseudo-purple, all mosaic or the two together.

In their inheritance, the pseudo-red of *Phaseolus* and the pseudo-purple of *Pisum* behave similarly, being transmitted to

the offspring negatively—a fact that has been pointed out with fragmentary materials even in early literature. Mixture of pseudo-monocolored seeds is a constant character in these plants, its frequency being virtually constant through generations. How, then, is the non-heritable variation accounted for? The gene responsible for the mottled character of the beans sets the plasm into a labile condition, or, in other words, pseudomutation occurs recurrently. Such cells, which should propagate *en masse* after cell division, develop into stripes on the seed-coat. Hirata (1934), who discussed the mottling from a purely physical standpoint, called attention to the fact that the stripes generally occur in somewhat rectangular patterns enclosed in a network of curved vertical and horizontal lines. This particular pattern is mainly owing to the characteristic mode of propagation of the colored epidermal cells and also to tension caused by the enclosed developing embryo. Pseudomutation occurs so frequently that all the seeds are striped and spotted; it, however, occurs at a relatively late stage of cell generation in the ontogeny of the testa, so that the mottling generally remains as stripes or spots. If it occurs early, the red color covers a larger surface of the seed-coat. Should pseudomutation arise before the formation of the primordia of the pod, all the seeds in that pod are pseudo-red; whereas should it occur somewhat later, different types of seeds are mixed together in the pod. As stated before, the pseudo-red seeds have small colorless parts on the testa, but not self-red, the colorless parts being due to the distribution of the colorless cells in the colored epidermis. Close inspection of the stripes of the mottled beans also reveals the presence of scattered white spots, as in the case of pseudo-red testa, from which it follows that the pseudomutated colored plasm is also labile, frequently reverting to the colorless condition, the back pseudomutation occurring so late in the ontogenic stage of the seed-coat that it generally results in spots. Recurrent pseudomutation is therefore reversible. The same principle of mechanism operates in the spotted and the pseudo-purple peas. In peas, however, the pseudomutation from colorless to purple occurs very late in the ontogeny of the testa, and its reverse also arises very late and with less frequency. It will thus be seen that the purple areas on the spotted seeds and the colorless parts on the pseudo-purple form spots. Transformation is also reversible. In both beans and peas, the differentiation due to pseudo-

mutation is renewed in passing through the stage of reduction divisions or gametophytic generation; the colored somatic cells thus producing colorless gametes, as in *Amaranthus*. Consequently, all the progeny plants from pseudo-monocolored seeds are mottled or spotted, no pseudo-monocolored individuals being obtained. It seems that in *Amaranthus* gametic or gametophytic pseudomutation occurs, producing self-red individuals; while in beans and peas this is not the case.

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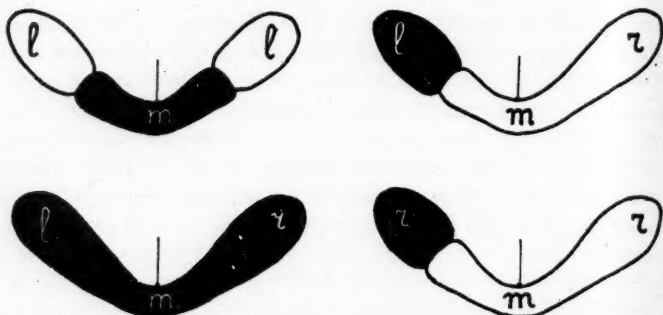
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INTRASPECIFIC ISOLATION ARTIFICIALLY
OBTAINED THROUGH CHROMOSOME
ABERRATIONS

THE present work was carried out with the aim of proving experimentally that it is possible to isolate from the principal species forms bearing chromosome aberrations. A new stock of *Drosophila melanogaster* is hereby described (Scheme 1). This structure was obtained as the result of crossing-over of the third chromosomes in females heterozygous for two reciprocal translocations between the second and third chromosomes. In one of these translocations—No. 302—the left end of the second chromosome is broken between *dp* and *b* and is exchanged for a distal part of the left arm of the third chromosome. In the other translocation—No. 228—the left end of the second chromosome is also broken between *dp* and *b*, but at the same time it is exchanged for a distal part of the right arm of the third chromosome. In females heterozygous for these translocations, crossing-over in the region of the third chromosome, which is located between the points of breakage, produces a structure in which both transloca-



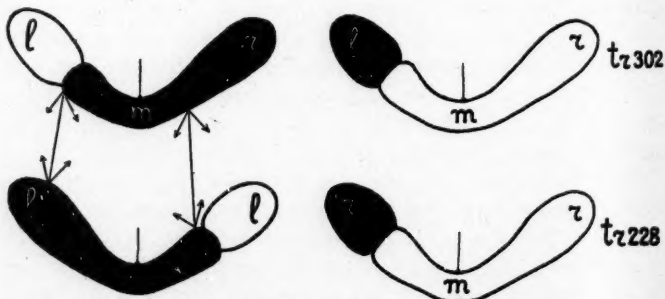
SCHEME 1. A newly obtained karyotype of *Drosophila melanogaster* ("Drosophila artificialis"). The third chromosome (both when entire and in cases of rearrangement) is black. The second chromosome is white.

m = middle portion of the chromosome.

r = right end.

l = left end.

tions from the second chromosome are located in the same third chromosome. If this complex chromosome (with two translocations) is present in an individual containing also a normal third chromosome and the two broken "second" chromosomes from both translocations, a normal chromosome balance is obtained and the fly possessing this structure is of normal viability. The author has obtained and is breeding such a stock. It breeds true to type, as a "balanced stock." If males from this stock are crossed with females from a normal stock of *Drosophila melano-*



SCHEME 2. Karyotype of a female heterozygous for both reciprocal translocations. The third chromosome and parts derived from it are black, the second one white. The arrows show the limits of the region located between the translocations. Crossing-over in this region causes the origination of a complex chromosome with two translocations.

gaster no progeny ensues, because in the flies of the artificial stock only hyperploid and hypoploid gametes originate which produce no viable progeny, when they fertilize orthoploid gametes. Our experiments have confirmed this. When females from this stock are crossed with normal males, a small progeny may be obtained as a result of single crossing-over in the third chromosome, in the region lying between the points of translocation. In this region crossing-over amounts to 1 per cent. Only 1 per cent. of eggs can therefore develop and 99 per cent. die. Experimental proof has been obtained that all the surviving specimens are single cross-overs. In the course of the breeding of this stock the hyperploid gametes of the females join the hypoploid ones of the males (and *vice versa*) and a normal chromosome balance is therefore established. This stock of *Drosophila melanogaster* is almost completely isolated from normal stocks. It is possible to isolate it completely by suppressing crossing-over in the region between the points of translocation, by introducing an inversion or the suppressor of crossing-over obtained by Gowen. In that case our new aberrant stock would be fully isolated from the initial species and would in this sense constitute a new species. In the near future a detailed paper will be published on this subject.

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INCREASED HEAT PRODUCTION IN A POIKILO- THERMOUS ANIMAL IN PARASITISM

In some former work of the senior author (1927) it was shown that snails infected with the larval stages of a trematode worm use more oxygen in a given time than do healthy ones in the same time. This was shown to be the case in the parasitism of *Physa occidentalis* by the various stages of *Echinostoma revolutum*.

Since such increased oxygen consumption accompanies parasitism, it occurred to us that there might be an increase, to a slight degree at least, in the heat output of snails showing the parasitized condition. The snail is a poikilothermous animal and has no mechanism for heat regulation, as does the warm-blooded animal. Any greater amount of heat generated in the augmented metabolic process going on in the parasitized snail

would perhaps be dissipated to the surrounding medium so that any net increase in the temperature of the snail itself would be slight, if any. That such an increase in heat output does occur in parasitized snails appears to be indicated by the experiments here reported.

Lymnaea stagnalis appressa (Say), a relatively large fresh-water form, was used in these experiments. Our specimens varied from 3.0 to 6.4 grams in weight as weighed to the nearest ten milligrams. This is an ideal species to use for such experiments because it is large enough to be easily handled and the temperature changes were of sufficient magnitude to be easily read.

A simple apparatus consisting essentially of a large tin can and three glass tubes was used for gathering data. This apparatus (Fig. 1) has the can (M) packed level-full with powdered asbestos (A). In the asbestos are embedded three heavy paper

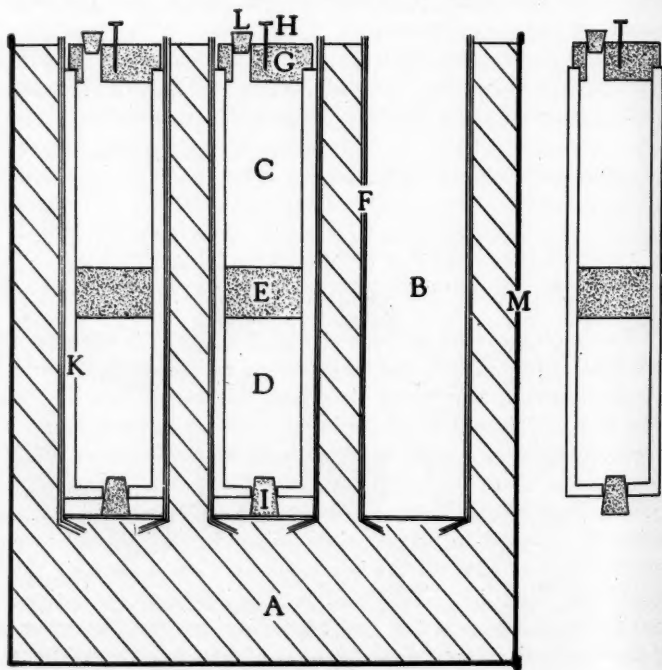


FIG. 1

shells made by rolling heavy wrapping paper (F) and into which fit moderately snugly three glass tubes (K). The bottoms of the shells are turned under and closed with cardboard disks to prevent leakage of the asbestos. For glass tubes we used glass filter mantles, the bottom holes of which were closed with corks (I). Such mantles are of thick glass and they are long enough to slide easily in and out of the paper shells. Since they were too long for testing chambers, a small chamber (C) of about 20 cc capacity was effected by driving corks (E) to a uniform depth down each tube. The spaces below the corks (D) are dead air spaces. One shell (B) is shown with the glass tube removed. The upper chamber (C) was stoppered with a tight cork with a small eccentric hole fitted with a small cork (L). This hole received the thermometer easily but snugly. A nail (H) in the stopper serves as a handle with which to remove the tube from the shell. The asbestos is held in place by a thin layer of asbestos plaster applied wet over the top around and between the paper shells.

The exact procedure in this series of experiments was as follows. Two (or one) snails were placed in a beaker of water that had been standing for twenty-four hours at room temperature. These were allowed to stand for one hour in order that they might have their temperatures equalized. They were then placed one each in two of the chambers of the apparatus and then all three chambers would be completely filled with water from the beaker. After one hour in the thermo-jacket the temperature of each chamber would be taken. A thermometer calibrated to 0.1° was used. It could easily be read to hundredths of a degree with a lens. Before taking each reading, the thermometer was allowed to stand for one minute in water at room temperature. By so doing the mercury in the thermometer stood at approximately the same point each time before using. In each case the small cork (L) was removed and the thermometer pushed to the bottom of the chamber. Water, as displaced from the chamber, was removed from around the thermometer with a medicine dropper to prevent it from wetting the paper jacket. The thermometer was allowed to remain in the chamber exactly two minutes before making the readings. After making the readings, the snails were removed, dried in paper towels and weighed. After this they were killed and examined under the microscope in order to determine the degree of parasitism or the lack of parasitism.

It was thought that since the snail is a poikilothermous animal and that since the variable quantities of heat that might possibly be produced in the diseased condition and in health would be transferred to the water, a measure of such heat could be effected by measuring increases in the temperature of the water containing the snails. Other factors than disease and health might enter into heat production. The degree of activity, or inactivity, of the snail would be a factor as shown by the senior author in a former paper (1927). Accordingly, an attempt was made to eliminate this factor in so far as possible in the present study by selecting snails that were fully active in all cases. The weight of each snail was also recorded, but no temperature relation could be ascribed to this factor. In fact, the coefficients of correlation between the weights of the two groups of snails, healthy and parasitized, and their individual temperatures are negligible quantities, being in each case *less than* $-.0005$.

The average weight of all the sixty-two snails that were used in these experiments was 4,400 mg and the average increase in temperature over the control was $.076^{\circ}$. For the 35 healthy snails the average weight was 4,029 mg and the temperature increase $.044^{\circ}$; for the 27 parasitized ones the figures are 4,881 mg and $.118^{\circ}$, respectively. So, according to these data, the parasitized group produced, on the average, a temperature increase in the surrounding water about 2.7 times that of the healthy group. The parasitized snails averaged 852 mg per individual heavier than the healthy ones. Due to the lack of correlation between weights and temperature, it is felt that the greater weight of the parasitized snails perhaps can not be placed in its proper relationship to the temperature data. However, it seems, regardless of this latter fact, and in view of the known fact of greater oxygen consumption of parasitized snails, to be reasonable to suppose that diseased snails actually do give up more heat to the surrounding medium.

In *Physa occidentalis* (Hurst, 1927) twenty-five healthy individuals averaged 0.0948 gram each in weight and consumed on the average 0.0366 mg of oxygen each in a four-hour period. A group of twenty-five parasitized snails of the same species averaged 0.0962 gram each in weight and consumed on the average 0.0392 mg of oxygen in a like period. *Physa occidentalis* is a much smaller snail than *Lymnaea stagnalis appressa*. The healthy specimens used in the present study averaged 4.029

grams in weight as against 0.0948 gram for the other small snail. The former average more than 42 times as heavy as the latter. The diseased specimens used in this study averaged 4.881 grams in weight as against 0.0962 gram for the other small snail. The former average more than 50 times as heavy as the latter.

It is interesting to note that in both the former study of the senior author (1927) and in the present experiments, the parasitized snails average heavier than the healthy ones. This can not be accounted for with any certain explanation. Work is being projected which will seek an answer to this question.

In one body of data, Hesse (1910) sets forth records of the oxygen consumption of *Helix pomatia* which varied from 13.49 to 62.59 milligrams per kilogram-hour with the average about 45 mg. In six *Physa occidentalis* selected at random (Hurst, 1927) the records range from 85.2 to 121.4 milligrams per kilogram-hour with the average at 103.4 mg. The disparity of the above figures may be due to the fact that *Physa* is a smaller and more active animal than is *Helix*. In *Lymnaea* no attempt was made to measure the oxygen consumption in terms of milligrams per kilogram-hour.

Since the temperature variations in the experiments reported here are quite wide, even in each group (healthy and parasitized), it would be of interest to know what effect the degree of parasitism has upon such variations. In the healthy group the temperature changes vary from 0.0° to 0.1° ; in the parasitized group from 0.05° to 0.33° . The latter group showed by far the greater variation. A certain degree of variation may be due to weight, activity and physiological conditions not controlled in the experiments. That such is the case is somewhat evident from the range of variation of the healthy group. Since the parasitized group showed such a large range, it is reasonable to suggest that the higher temperatures are associated with parasitism. No attempt was made to check the degree of parasitism accurately. However, it may be pointed out in passing that the three snails showing the greatest temperature change (No. 40, 0.33° ; No. 45, 0.28° ; and No. 47, 0.2°) are recorded in the notes of the experiments as showing the three cases of heaviest infection. These cases were so heavy that they were unusually striking.

SUMMARY

The experiments herein reported seem to indicate that parasitism of *Lymnaea stagnalis appressa* by the larvae of trematode worms causes the snails to generate and to lose more heat to the surrounding medium than do healthy ones. On the average, they raise the temperature of a small quantity of water about 2.7 times as high as do the healthy snails.

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CHROMOSOME CONFIGURATIONS IN OENOTHERA
(GRANDIFLORA \times LAMARCKIANA)¹

IN 1930, the writer found that when *excellens* (from *chicaginesis*) is combined with *Devil's Gate*, *Dalton* and certain other genoms belonging to races from California, the resulting hybrids have 7 pairs in diakinesis, thus showing that *excellens* has the same arrangement of terminal chromosome segments that these genoms have. He also found that *Devil's Gate* and *Dalton* give a circle of 4 when combined with *acuens* (from *grandiflora*), and on the basis of these findings predicted that *excellens . acuens* would be found to have a circle of 4, and 5 pairs. When these data were transmitted to Dr. A. H. Sturtevant privately, the latter called the attention of the writer to the fact that they were not in harmony with certain previously reported data with regard to chromosome configuration, namely, with the presence of a circle of 10 in *excellens . gaudens*² and a circle of 14 in *acuens . gaudens*.³ Dr. Sturtevant pointed out that the latter data imply that

¹ Aid has been received from the Joseph Henry Fund of the National Academy of Sciences and the Penrose Fund of the American Philosophical Society.

² Cleland and Blakeslee, *Cytologia*, 2: 175-233, 1931.

³ Cleland and Oehlkers, *Jahrb. f. wiss. Bot.*, 73: 1-125, 1930.

excellens and *gaudens* have 2 chromosomes in common (i.e., with the same segmental arrangement), but that *acuens* and *gaudens* have no chromosomes in common. Therefore, if *excellens* . *acuens* has a circle of 4 and 5 pairs, as suggested, i.e., if *excellens* and *acuens* differ in respect to 2 chromosomes and only 2, then these must be the 2 which *excellens* has in common with *gaudens*, and which therefore can not be present in *acuens*. But if this be true, then *acuens* . *gaudens* should have circles of 10 and 4, and not a circle of 14.

The writer proceeded to reexamine all data. All slides upon which these data were based were restudied, and all were found to have been correctly interpreted. Elimination of this possibility of error left but 2 further possibilities, either (1) that cytologically atypical material had been unwittingly used at some point, or else (2) that an error had been made in diagnosing certain plants in the field.

The following summer, material was accumulated which showed that the error had apparently been made in respect to the configuration of *acuens* . *gaudens*, and not in respect to the configurations of the other combinations concerned. In the first place, the F_1 of the cross *chicaginensis* \times *grandiflora* was grown, and it was found that *excellens* . *acuens* had the circle of 4 and 5 pairs predicted for it. Furthermore, crosses of *Devil's Gate* and *Dalton* with *lamarckiana* showed that *Devil's Gate* and *Dalton* both give a circle of 10 with *gaudens*, and that therefore the reported configuration for *excellens* . *gaudens* was correct. Consequently, the cross *grandiflora* \times *lamarckiana* was remade (using *r-lamarckiana*), and the F_1 grown in 1933. All 4 complex combinations were present. Examination of their chromosome configurations gave the following results: *acuens* . *velans* had circles of 4 and 6 (as previously reported); *truncans* . *velans* had a circle of 4 and 10 (as previously reported); *acuens* . *gaudens* had a circle of 12 (vs. a circle of 14, as previously reported); *truncans* . *gaudens* had a circle of 14 (vs. circles of 10 and 4, as previously reported).

The two laetas in this cross are easily confused in the field by reason of the fact that *gaudens* almost completely masks the characters of both *acuens* and *truncans*. Consequently, when the previous study was made,³ we were uncertain as to our diagnosis of the laetas (see Cleland and Oehlkers 1930, p. 49, 2d par.). It is evident from the reexamination of this material that *trun-*

cans. gaudens was mistaken at that time for *acuens. gaudens*, and that *acuens. gaudens* was either absent or was not recognized.

The chromosome configurations as now revised offer no difficulties from the standpoint of segmental interchange, for they all fit in with what is known concerning the segmental arrangements of the complexes in question.

The segmental arrangement of *acuens* is now definitely and completely determined. Since it gives 2 circles of 4 with *hookeri* and one circle of 4 with *flavens*, it must have 2 more chromosomes in common with *flavens* than with *hookeri*. The only two *flavens* chromosomes not found in *hookeri* are 1·4 and 3·2, which *acuens* must therefore have. Since *acuens* gives one circle of 4 with *excellens*, it must have 2 more chromosomes in common with *excellens* than with *hookeri*. These must be 7·10 and 9·8, since these are the only *excellens* chromosomes absent in *hookeri*. *Acuens* has 3 chromosomes in common with *hookeri*. Since it has 1·4 3·2 7·10 9·8, the only *hookeri* chromosomes left which can be common to *acuens* are 5·6 11·12 13·14. The entire segmental arrangement of *acuens* is therefore known. It is as follows:

$$acuens = 1 \cdot 4 \ 3 \cdot 2 \ 5 \cdot 6 \ 7 \cdot 10 \ 9 \cdot 8 \ 11 \cdot 12 \ 13 \cdot 14$$

The foregoing statement emphasizes with peculiar force the correctness of the segmental interchange hypothesis as applied to *Oenothera*, for when it is possible by the application of this hypothesis to detect and correct errors in the identification of genetic material, there can be little doubt as to the validity of the hypothesis.

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A STUDY OF INDIVIDUALITY IN THE NUTRI- TIVE INSTINCTS AND OF THE CAUSES AND EFFECTS OF VARIATIONS IN THE SELECTION OF FOOD†

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THE recognition of individuality, or the discernment of differences in form and function between individuals of the group, has been responsible for a large part of the progress made by biologists in understanding the nature of living things. Each successful resolution of the ap-

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† Paper from the Biological Laboratory, Experiment Station, University of Maine, No. 209. Published with the approval of the director of the station, 20 June, 1935. This analysis of the problems related to the nutritive instincts and associated phenomena represents one phase of a study on the relation of man and animals to their environment, planned (1927) and directed by the writer as a Purnell project at the Maine Experiment Station. The project as a whole represents an attempt to treat an ancient as well as modern but heretofore highly speculative anthropogeographical problem from a strictly scientific and experimental point of view. Since the extreme diversity in the nutrient environment of animals contributes to variability in form and function and to survival, and since man like animals is highly affected in turn by his environment, by his reactions toward food and by social and economic pressures related to food-getting, we can look upon these problems as twice pertinent to man, who can not with such readiness as animals be experimented upon.

‡ The writer is highly indebted to a number of persons who from time to time have assisted him in the prosecution of these experiments: To Mrs. Emmeline Kenney for assistance throughout the entire period in securing the experimental data; to E. R. Tobey, chemist, for the chemical analysis of food used in the experiments; to Miss Mildred Covell and others for calculations on the data secured; and to Ruth Stone Dove for constructive assistance with the manuscript.

parently erratic action of individuals into a predictable system that may be reapplied to the group has served as a spur to new research. As in the past, so in recent times those contributions which have most clearly guided biologists into an ever-expanding and more accurate appreciation of the phenomena of life have been those discoveries or points of view rooted in a new appreciation of the *individual*. For example, the observation of Darwin (1859) that species could evolve one from another by the gradual accumulation of slight differences between individuals, the recognition by Galton (1869) of innate intellectual differences in man, the measurements by Cattell (1885) and later by James of psychological individual differences,¹ the discernment by Bateson of an immense diversity between individuals in form and function, the attempts by de Vries to codify persistent individual mutations and the final successful interpretation of Mendelism by the Morgan school as a mechanical individual gene-chromosomal schema of inheritance—each analysis in terms of the individual resulted in a new advance in control over living forces. And by virtue of such recognition, individuality, or the unit character, or its chromosomal representative the gene, exists to-day embodied in the basic concepts of a number of biological and associated sciences.

And yet with all these contributions to its credit the great potentialities residing in this concept of individuality have scarcely been tapped. The present trend toward generalization, the present desire to bury the individual in the group has tempted science from the inductive method based upon the individual to the deductive based upon the group. Many of the experimental procedures of to-day with both animals and plants are based upon a certain "security in numbers," upon the "average genotype," or upon nullified individualities as found in the concept of the "pure line" or the "homozygous stock" represented by a type secured through chance selection

¹ The term "individual differences" was first used by J. McKeen Cattell.

or survival. Furthermore, "statistical technique" has turned the eyes of many toward a mirage of results based upon means and probabilities, of conclusions stated in terms of average individuals or average populations or average expectancies.² As a result, science has been in many instances almost completely blinded to the importance of individual differences.

During the past seven years the writer has attempted to apply the concept of individuality to the experimental analysis of certain biological problems which have heretofore been considered problems for mass technique. The experiments have been concerned with individual differences in the most powerful of all instincts³—those of

² One of the many examples of this difficulty with individual variability may be found in a report by E. W. Sheets ("Meat Research in the United States," *Scientific Monthly*, January, 1934, pp. 50-59). He says (p. 57): "Another difficulty has been the individual variation in the inherent character of the experimental animals. There is more difference between individual animals in the same lot than between the averages of the two lots. We are forced to use larger numbers in each lot; to depend upon the law of averages to offset the error of individual variation until more uniform experimental animals can be produced." A method was suggested by the writer (Dove, 1930) whereby these difficulties could be in part eliminated by means of a series of individualized inbred strains, each strain selected for a different degree of expression of the character. A similar method has been adapted to the problem presented in the present paper.

³ The term "instinct" has received severe condemnation of late from many sources, and perhaps rightly so, for the term has been used loosely to identify phenomena known more properly by some other term, has been employed as a generalized term for indefinite processes and has even been grossly misapplied. The writer holds no brief for or against the term "instinct" and he considers no faculty psychology possible in relation to the complex of food-seeking and food-getting. However, he finds the pluralized term "nutritive instincts" a convenient one to express the entire gamut of those genetic factors which through the medium of natural selection operate upon food-seeking.

Let it be emphasized that the data presented in this paper are experimental facts pertaining to a definite end-result (growth) in terms of weights and measures. It is hoped that from these facts information may be gained as to the relative value of the genetic, the nutritional and the social factors contributing to the end-result. It appeared to the writer that a genetic analysis of those factors in food-seeking and food-getting which are hereditary, in short, a genetic analysis of certain factors called "nutritive instincts," would supply the behaviorist with a forceful tool for prying into the general nature of drives and "purposive" behavior in animals and man

food-seeking. More perhaps than any other phase of biological activity these instincts promised to furnish a great variety of individual reactions, for, in addition to the drive for food as such, there is discernible among any group of individuals definite desires for particular foods. These desires may be normal or the result of perversion; they may be expressed as cravings for nutrients deficient in the food available, or as habits which, having been formed during early life through chance or social influences, have persisted harmfully or harmlessly into maturity. When examination is made into the nature of these variations, there is found a consistency in the desires for special foods which indicates the presence of physical, biological and social principles controlling their expression.

Observations on the behavior of the experimental animal when given free opportunity to choose his own food have already been made by various workers. Nutritionists have, from time to time, "discovered" that the ability of animals to choose their own food is apparently superior to the ability of the nutritionist to formulate a ration or a diet scientifically. Davis (1928, 1933), as a result of many years' experiments on infants, has recently recommended the free-choice method of feeding children. This method of feeding the infant has countless forerunners in the extensive literature on the so-called "free-choice" feeding of farm animals⁴ and in some carefully controlled

and for distinguishing the potentiality of innate abilities from the effect of the environment.

⁴ Only a very few of the tests on the feeding of farm animals reported as "free choice" are in reality free choice. In many instances the tests are made with roughage and a grain mixture, and the term "free choice" is used to indicate the fact that the animal has freedom to consume as much of the grain mixture as it desires. Furthermore, even in some of the more carefully controlled experiments on the free selection of food, the check rations used for comparison are not wholly all-mixed but represent mixed rations in addition to which there is permitted to the animal freedom to secure salt, minerals or roughages. For these reasons, only a very few of the large number of tests reported on this subject are applicable to the present problem of free selection of food.

experiments on laboratory animals, such as the work of Evvard (1915) with swine, Pearl and Fairchild (1921) with poultry, Nevins (1927) with dairy cattle, and Harris et al. (1933) with the laboratory rat. Conclusions vary. Evvard, Pearl and Fairchild, and Davis conclude that animals and the child sometimes appear to thrive as well, or better, when permitted a free selection of food as when fed a scientifically devised ration used for comparison. Harris, on the other hand, in one of the few strictly vigorous attempts to analyze the problems of food selection, has come to the somewhat discouraging conclusion that experience and habit control the choice of food and that since habit is based upon the vagaries of the individual the free choice of food can not be used as a guide for food requirements.⁵

Up to the present time a final conclusion as to the relative merits of the instincts of nutrition and the science of nutrition could not have been justified, for on the one hand the nutritionist is continually improving in his ability to devise rations and on the other hand the nature of the nutritive instincts and the nature of the factors which cause seemingly unreasonable vacillations in expression have not been thoroughly analyzed. Such an analysis may reveal much of value. For example, even though experience and habit must be considered strong influences in preventing nutritional readjustment, as Harris states, nevertheless both experience and habit, if properly directed, perhaps may be made to serve well the purpose which they were designed by nature, through survival, to serve. Furthermore, there appear to be factors other than experience and habit which enter into the expression of food desires, factors related to the innate drives of different genotypes. Individual differences in reactions to

⁵ A number of reports on the free selection of food have appeared within the last two or three years as studies in animal behavior. Frequently these studies are made on the order of preference for different foods without regard to the quantity and quality of food consumed. Young (1933 b), however, has recognized the significance of the biochemical aspects of the problem.

food are, it is believed by the writer, an expression, in part, of innate genetic individuality.

Heretofore scientists have neglected to apply the concept of individuality⁶ to their study of the nutritive instincts, and to consider seriously the individual variations in food selection. Although individual differences in reactions to food have been noted by a number of workers, no value has ever been assigned to such differences. In this paper the writer proposes a genetic, behavioristic and mechanistic interpretation of these individual differences in the choice of food.

Such an interpretation seeks to analyze the expression

⁶ The term "individuality" is applied, throughout this paper, to the actual measurable differences between individuals. Differences in growth rate are obviously due to both genetic and environmental factors or to an interaction between the two (psychological factors are included with genetic and environmental interactions). In this sense individuality represents a *result* that may be duplicated from a number of combinations of causes.

When observations are made on the growth rate of any group of apparently uniform animals allowed a free choice of food, the individual growth rates will be found to fluctuate about a mean in the form of a normal frequency distribution curve. The smallest individuals will be significantly smaller than the largest. The two extreme individuals will appear as of different strains or even as belonging to different breeds, so great sometimes are their differences.

Some of these differences in growth rate we can attribute to a small indefinite amount of heterozygosis of the genetic factors for growth rate. But a large part of the differences must be attributed to non-genetic factors or to a combination of genetic and environmental factors. I have chosen to express the cause for some of these differences by the term "wisdom" or "lack of wisdom," *i.e.*, wisdom in regard to the choice of both quantity and quality of food. Wisdom in one sense is synonymous with the possession of abilities to choose that food required for the optimum expression of the genotype or phenotype.

In so far as the nutritive instincts have a genetic basis, wisdom will be directly related to the securing of the proper nutrition for any particular phenotype. But in so far as abilities to choose food are influenced by accessory factors, such as habit, experience, imitation, dominance-submission, etc., and in so far as the individual fails thereby to secure the nutrients required for optimum phenotypic expression, he will be classed as unwise. Unwisdom, then, may be due to a lack of instinctive reactions, but the same effect, as of unwisdom, may be caused by environmental factors which distort the normal functioning of the instincts. These foregoing considerations clearly emphasize the double nature, genetic and environmental, of wisdom, and of the expression of the nutritive instincts.

of food demands by individuals of varying genetic complex placed in different social relations and in different environmental situations. The problem as a whole, then, is concerned not alone with experience and habit, with cravings to supply nutrient deficiencies, with depraved appetites and perverted hunger, with the effects of environment and accessibility to food, but especially with the food desires of individuals whose differing genotypes drive them toward different degrees of biological function or differences in form. Changes in form or function, it is logical to conclude, will be accompanied by differences in choices of food. It is true, of course, that such changes may also be accompanied by differences in the quantity of food consumed. Within certain limits an animal may increase or decrease a function by varying the quantity of food consumed—or may partially submerge the qualitative deficiencies of food by quantitative variations.⁷ However, a certain equilibrium would doubtlessly be sought between an excess of one nutrient factor and a deficiency of another factor. Regardless, then, of certain quantitative partial adjustments, the ratio of nutrients selected for a particular function still persists, and the native ability of the animal may thus be expressed in a desire for foods required for the expression of individual differences in bodily form and function. Furthermore, the obverse is true: That differences in consumption of foods produce differences in form and function. The effect, on the one hand, of the individual gene-determined desires for food upon form and function and the effect, on the other hand, of the foods selected upon form and function (including the desires for food) are here recognized in the expressions of individuality.

⁷ For example, an animal may require 5 grams of calcium a day for a particular function. If the ration contains 5 per cent. of net available calcium, then 100 grams of food per day will be required. On a ration containing only 4 per cent. of calcium, a larger quantity, *i.e.*, 125 grams of food per day, will be needed in order to meet the requirements and prevent a negative calcium balance. In this manner larger quantitative consumption may bury qualitative deficiencies.

REPORT OF EXPERIMENTS

It is evident that a nutritional study, probably any experimental study, of individual differences can not legitimately be made on single, isolated individuals (except for comparative purposes), since most of the common experimental animals are social creatures and are considerably affected by social interactions in the amounts and choice of food consumed. In order to give the proper recognition to individuality and at the same time to bridge isolation and retain the social group intact, the writer found it necessary to break away from older standard methods of animal experimentation. Therefore, in distinct contrast to the commonly accepted biological techniques in which *the individual must conform to the group* (by use of the homozygous strain or the random grouping), *the group was made to conform to the individual*. The group conforms to the individual when all members of the group are substantially alike in the character to be tested and when each group differing from other groups as individuals differ is treated experimentally as a unit. In this way, the form and the destiny of the individual completely determines the form and the destiny of the group. This technique permits a full and free expression of individuality in a social grouping, and as far as the social factor is concerned the results are not subject to the excessive distortion which would characterize an attempt to analyze the problem with isolated individuals.⁸

The present discussion is confined for brevity to records secured on the chick, although the same experiments are in progress in this laboratory with a number of different species of animals. Over 3,000 chicks have been used in preliminary work for the basis of the results presented here in summary form.

⁸ This method of grouping individuals of a kind together will alter the behavior to the extent that more of the individuals who would generally be leaders will probably be grouped together among the superior, while those who would generally be followers will probably be grouped together among the inferior.

The final experiments here reported have been carried out in an especially constructed experimental laboratory under carefully standardized conditions: uniform cage size, feeds used, feeding tray space, alternation of feeding tray positions, feeding interval, light intensity, temperature, source of stock.

The records have been taken with a view to analyzing the association between the expression of the nutritive instincts and all biological activities in any way dependent on or influenced by the nature of the food consumed. However, the present analysis will be confined principally to one biological activity, *i.e.*, to the growth rate during the fastest-growing period of life, from three to eleven weeks of age, during which time the birth weight is multiplied from nine to ten times. Those genetic and environmental factors which express themselves in rate of growth may normally be expected to cause wide variations in the average rate of growth during this period—variations approaching a magnitude of 300 per cent. Thus in analyzing growth, we shall be analyzing a character which is known to be highly modified by both genetic and nutritional factors and which may be readily measured by growth rate and by the food energy, minerals and vitamins selected for each individual rate of growth.

PREDICTION OF GROWTH RATE AS THE MEASURE OF INDIVIDUALITY

The innovation in the experimental method of grouping individuals has been determined by a growth relationship of high importance: namely, the fact that the *immediate* future growth rate of young animals can be predicted with a significant degree of accuracy prior to the experimental period. The growth rate of an individual chick in any period of two weeks (considered the optimum length of period) is correlated with the growth rate in the succeeding two-week period by an r of from 0.48 to 0.64, as is shown in Table I.

By taking advantage of this correlation between the rate of growth made in a preceding period and the im-

TABLE I
CORRELATION BETWEEN GAINS IN WEIGHT BY CHICKS DURING
SUCCESSIVE TWO-WEEK PERIODS

Age intervals				Coefficient of correlation (r)	n
1st week to	3rd week with	3rd week to	5th week	0.6399 \pm .0407	96
3rd " " 5th	" " 5th	" " 7th	" " 7th	0.5787 \pm .0476	89
5th " " 7th	" " 7th	" " 9th	" " 9th	0.6230 \pm .0440	88
7th " " 9th	" " 9th	" " 11th	" " 11th	0.4827 \pm .0554	87
9th " " 11th	" " 11th	" " 13th	" " 13th	0.5596 \pm .0502	85

mediate future rate of growth, we find it possible to select those individuals which may reasonably be expected to grow the most rapidly during the ensuing two-week period. Likewise individuals which will grow more slowly may be sorted out—each type of growth rate in a separate group. In this manner a series of groups of individuals may be arranged in a descending order determined by the bodily gain to be expected during the coming two-week period.

At the end of each two-week period the large group of 100 individuals was reassorted into 10 small groups of 10 individuals, the groups graded according to the predicted rates of growth to be made in the next two weeks. This same reassortment was made for each of the four two-week periods until the chicks were eleven weeks of age. In this way, at the end of each two-week period a group of the ten fastest-growing individuals and a group of the ten slowest-growing individuals had been separated out with a graded series of eight groups between the fastest- and the slowest-growing groups.

The food preferences shown by such a series of groups expressed a serial order in the type of food required for fast versus slow rate of growth. Proof for the veracity and value of the test was made by the subsequent feeding of a mixture of the foods indicated by these individualized groups to ten groups with identical future growth rates predicted for them.

THE "WEANING" PERIOD

These experiments, as stated before, have been made upon chicks started at 3 weeks of age. Numerous difficulties encountered in the attempts to bridge the gap from 0 to 3 weeks of age precluded the use of an age earlier than 3 weeks in the experiments here reported. There are perhaps several causes for the difficulties. First, before 3 weeks of age the maternal yolk has usually not been entirely absorbed and the chick is therefore living in part on stored energy. There is some evidence that this stored energy from the yolk affects the response of a chick to its environment (Dove, 1934, pp. 220-222). For this reason the first 3 weeks are termed the "weaning" period. Second, it is possible that the first few weeks of life, besides being a time of weaning from the maternal yolk and of special bodily demands, may be a period either of maturation or of learning or of both. The existence of such a period of maturation or learning is suggested from an analysis of the changes in food selected as age advances. In Table II and in Fig. 1 are shown the results of this analysis.

TABLE II
RELATION BETWEEN AGE AND CHOICE OF FOOD (100 CHICKS)

Age	Corn meal	Fish meal	Bone meal	Oyster shell flour	Wheat bran	Wheat mid-dlings	Oat meal
0 - 3½ days	29.5%	6.3%	3.0%	.7%	12.6%	14.4%	33.6%
3½ - 7 "	32.5	7.9	4.4	.9	12.8	10.3	31.0
7 - 14 "	30.6	7.7	3.8	.7	18.3	4.7	34.2
2 - 3 weeks	47.4	8.6	2.4	.1	11.9	4.0	25.6
3 - 5 "	57.3	7.9	2.3	1.1	10.1	2.3	19.0
5 - 7 "	61.9	9.4	2.2	.7	12.6	2.2	11.0
7 - 9 "	65.4	10.2	2.9	.8	11.7	3.2	5.8
9 - 11 "	67.1	11.5	3.6	.9	9.7	1.7	5.5
11 - 13 "	68.9	13.1	4.1	1.6	8.0	1.4	2.9

It may be observed from Fig. 1 that, at hatching time and for the first week or two after hatching, the different foods were selected more nearly in equal quantities than at any time later. Corn, which in later life was consumed

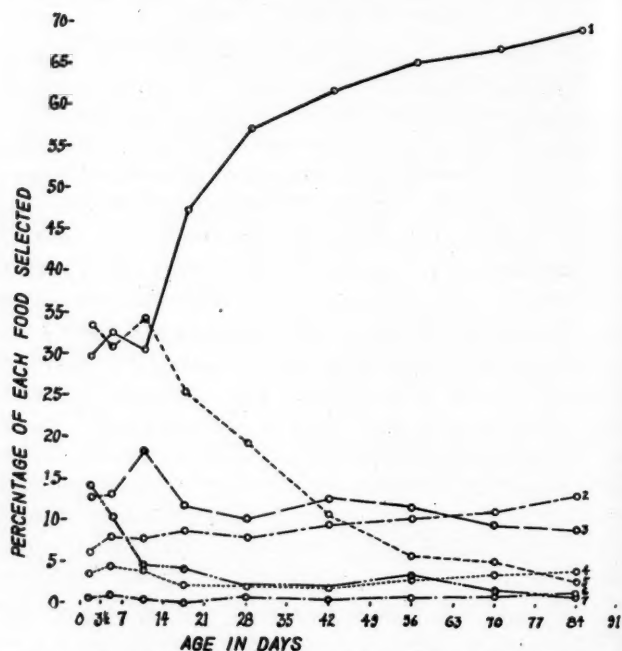


FIG. 1. The relation between age and choice of food shown graphically from data presented in Table II. The records are based upon the average consumption of food of 100 Rhode Island Red chicks from 0 to 91 days of age. The foods are numbered as follows: 1= Yellow Attrition Corn Meal; 2= Fish Meal (white fish and herring, vacuum dried, biologically assayed as a source of vitamin D); 3= Wheat Bran; 4= Bone Meal; 5= Oat Meal; 6= Oyster Shell Flour; 7= Wheat Middlings. The ratios of foods chosen during the first few weeks tended to differ strikingly from the ratios of foods chosen in the later periods of the growth cycle.

in relatively *large* amounts, was at hatching time consumed at a *lower* rate, while bran, middlings and oats, which in later life were consumed in relatively *small* amounts, were at hatching time consumed at *higher* rates. In other words, these four foods were selected at first more nearly as though all foods are alike and, as the period progressed, each food was gradually given favor or disfavor—either because the chicks' ability to choose improved or because their judgment was gaining in ac-

curacy through experience.⁹ These statements in regard to the shift in food choice did not always hold, since one food (fish) was chosen in ever-increasing amounts with advancing age, even though it was consumed at first at a very low rate. Neither do these statements mean that *no* discernment is present at the first (or second) contact with food, but they do indicate that there may be less ability to judge food differences at hatching time than later.

In those experiments in which chicks were fed a mixture of foods for the first 3 weeks and were only then permitted free selection of foods, they tended, when finally permitted to choose food at will, to consume foods in ratios in keeping with their age or stage of development (Table VI). Thus chicks seem not to be required to learn from experience or else learn very rapidly.

These difficulties emphasize the fact that the first 3 weeks of the chick's life cover a period that must be dealt with in a special manner. Experiments now in progress are gradually bringing this period under control through the collection of data which indicate that normal maturity may be attained by the proper assortment of foods for free selection from 0 days of age. But since a measure of the complete success in control over this early period requires a notation of the effects as represented in later activity and in longevity, several years must pass before it can be stated that this period has definitely been brought under satisfactory control.

FOODS USED IN THE EXPERIMENTS

The different foods used in the experiments were limited to the lowest possible number, since an excess of foods with a duplication of source of nutrients would confuse the results. In an attempt to find the assortment of foods which, few in number, would support normal growth and development under carefully controlled experimental

⁹ Bird (1933) has shown that accuracy in picking up food increases with the age of the chick for at least 20 days—and that this accuracy is gained in part from experience and in part from maturation.

conditions, several thousands of chicks were used. In some of these preliminary experiments purified foods were tested, but in the experiments here reported only naturally occurring foods commonly fed to chicks were used: First, because so-called "purified" foods, and "chemical" foods, far from being completely purified, are generally contaminated with small quantities of extraneous materials well within the range of detection by the taste glands of experimental animals, and second, because it was desirable to study the nature of food selection under the most natural conditions possible.

The final decision as to the correct assortment of foods was determined entirely by the results secured. Food combinations which failed to prevent deficiency diseases in the majority of individuals were eliminated and only those foods were included which contributed in one or more ways to the health and vigor of the experimental animals which were wise enough to make the proper choice.

The final assortment of foods included the following:

Plant Source: Yellow Attrition Corn Meal, Wheat Bran and Ground Oat Feed.

Animal Source: Dried Skim Milk Powder and Maine Fish Meal (White Fish and Herring).

Mineral Source: Ground Bone Meal Flour and Oyster Shell Flour.

The foregoing list of seven foods proved to be an assortment from which the most superior individuals were able to choose rations which would not only bring them up to sexual maturity within the normal period of time in a sunless laboratory—a result difficult to accomplish with mixed rations—but would also sustain life and reproduction. The less wise, unfortunate and inferior individuals, on the other hand, were afflicted with various forms of deficiency diseases according to their failure to consume the correct ratios and quantities of the seven foods before them.

Furthermore, the foods adopted are foods which will be eaten by a large number of species of laboratory animals, such as the mouse, the rat and the chick, and by domestic

TABLE III
COMPARISON BETWEEN THE RAT AND THE CHICK IN THE
CHOICE OF FOOD FOR GROWTH

Foods	Rats*	Chicks†	Chemical constituents	Rats	Chicks
Corn meal‡	72.61%	52.8%	Water	10.04%	9.67%
Fish meal	3.23	11.4	Ash	4.47	6.83
Bone meal	1.15	2.9	Protein	13.92	17.90
Oyster shell flour95	.6	Fiber	2.89	3.63
Wheat bran	11.00	21.3	N. F. E.	61.26	54.79
Skim milk powder ...	5.99	2.1	Fat	4.31	5.76
Oat meal	5.07	8.9	Salt18	.62
			Lactose	2.96	1.04
			Calcium813	1.301
			Phosphorus626	1.058

* Records based on food selection of 16 white rats from age of weaning (4 weeks) to sexual maturity (12 weeks).

† Records based on food selection of 50 Rhode Island Red chicks from 0 to 11 weeks of age.

‡ 99 parts of Yellow Attrition Corn Meal plus 1 part of Cod Liver Oil.

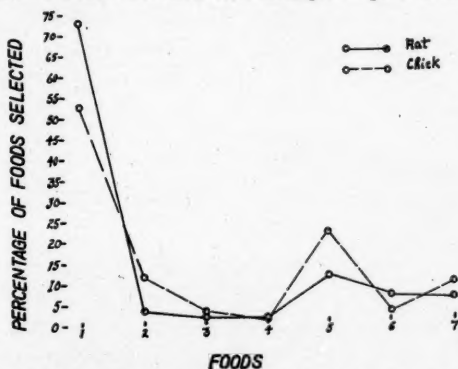


FIG. 2. Comparison between the rat and the chick in choice of food during the period of growth. The foods are numbered as follows: 1 = Yellow Attrition Corn Meal (1 per cent. Cod Liver Oil); 2 = Fish Meal; 3 = Bone Meal Flour; 4 = Oyster Shell Flour; 5 = Wheat Bran; 6 = Dried Skim Milk; 7 = Oat Meal.

The rat and the chick have some strikingly similar preferences for certain foods. The two species prefer corn meal to all other six foods; wheat bran to oat meal; bone meal to oyster shell flour. But despite these similarities of preference, each species consumes a total ration with a chemical composition which in some of its details indicates that each is securing the nutrients required for a specialized type of body growth, a result which might be expected.

animals, such as swine and (with modifications) cattle and other ruminants. The same foods are representative of those supplied to human beings. A study of the behavior of different species in reaction toward the same foods reveals some striking similarities as well as differences. These similarities and differences are as consistent as are the choices made by like individuals of the species. The problem of inter-species differences and similarities in the choice of food will be considered in a later paper. In Table III and Fig. 2 are data secured for the growing period on the rat and the chick which give a concise indication of this problem. While the serial order for the consumption of corn, bran, oats, bone meal and oyster shell flour was the same for both rat and chick, nevertheless, the total food rations consumed by the two species differed strikingly in protein, ash, calcium and phosphorus percentages.

EXPERIMENTS TO DETERMINE THE RELATIONSHIP BETWEEN FOOD PREFERENCES AND GROWTH

In order to determine the relationship between food preferences and growth, four batteries of 100 chicks each were given the opportunity to select their rations from the seven foods listed in the foregoing section. Each group of 100 chicks was treated as a unit and was redivided into 10 groups of 10 each in serial order according to the gains which were predicted for each individual and group in the succeeding two weeks. Two batteries of 100 individuals each were run simultaneously for a check upon the consistency to be expected when the food was exactly identical. Two other groups were run, each at different times, in order to secure the additional effect of seasonal or other factors concomitant with new supplies of foods. The chemical constants for the foods used may be found in Table IV.

Data were taken in terms of individual bi-weekly body weights and bi-weekly gains in weight. Food records were taken in terms of actual food consumed per group and in terms of percentages of each food selected during

TABLE IV
CHEMICAL CONSTANTS OF FOODS USED IN FREE-CHOICE EXPERIMENTS*
(In parts per hundred)

Foods	Moisture	Ash	Protein	Fiber	N. F. E.	Fat	Salt	Lactose	Ca	P
Corn meal ...	10.90	1.33	9.69	2.19	72.04	3.85			.013	.269
Fish meal ...	7.07	17.82	54.47			17.70	5.43		3.330	2.193
Bone meal ...	7.15	63.52	25.35			2.99			21.914	10.828
Oyster shell flour21	97.56							37.044	.556
Wheat bran	9.56	6.02	16.99	9.80	52.53	5.10		49.46	.105	1.348
Skim milk powder ...	5.58	8.14	35.44			.98			1.260	.960
Oat meal	8.40	2.39	16.59	4.33	62.51	5.78			.097	.472

* The figures represent averages of samples of food taken during the seventh week of each experiment. The values for calcium and phosphorus content of corn meal, bone meal, oyster shell flour and wheat bran were calculated from the ash content. Calcium and phosphorus content of fish meal, skim milk powder and oat meal were secured on single samples taken during the course of the experiment.

each two-week period. In order to determine the mathematical relationship existing between gain in weight and proportions of foods selected, regression lines were passed through the data on food selection according to a regression equation¹⁰ with direct reference to the actual average gain made by each group.

The theoretical percentages of foods secured for the two most extreme groups (the fastest- and the slowest-growing) were then used as the extremes of the test experiments (Table V).¹¹ In the test experiments, mixtures

$$^{10} Y = My + [(mx - \text{origin of } x) \cdot a]$$

$$= My + x^1 \cdot a$$

when Y = calculated y value when x is the least

x = group average gain in weight for the two-week period

y = percentage of food consumed

x¹ = deviations of x from the mean of x

$$a = \frac{\sum x^1 y}{\sum (x^1)^2}$$

or the slope.

¹¹ Space prevents the tabulation of all the 200 different rations concerned in these experiments. The lists of foods selected by the slowest- and the

of foods in the same proportions were fed to groups of chicks assorted equally according to the predicted gains in weight to be made. Between the two extreme groups there were placed 8 other groups, each calculated to produce a growth rate different from that of every other group, in a serial order from lowest to highest at equal intervals apart. Regression lines were not run through the series of group gains in weight. These averages tended to flock about a mean in the manner of a Gaussian frequency distribution with the values for both the slowest- and the fastest-growing group spaced widely as in tale frequencies. A regression line passed through such growth rates might occasionally produce for these tail-end groups theoretical values not met in nature, values which could not be used in the proof tests on mixed foods. But with the method followed, it was certain that the two most extreme groups, the fastest- and the slowest-growing, could be duplicated—and thus these two groups automatically came to form the boundaries of the proof test.

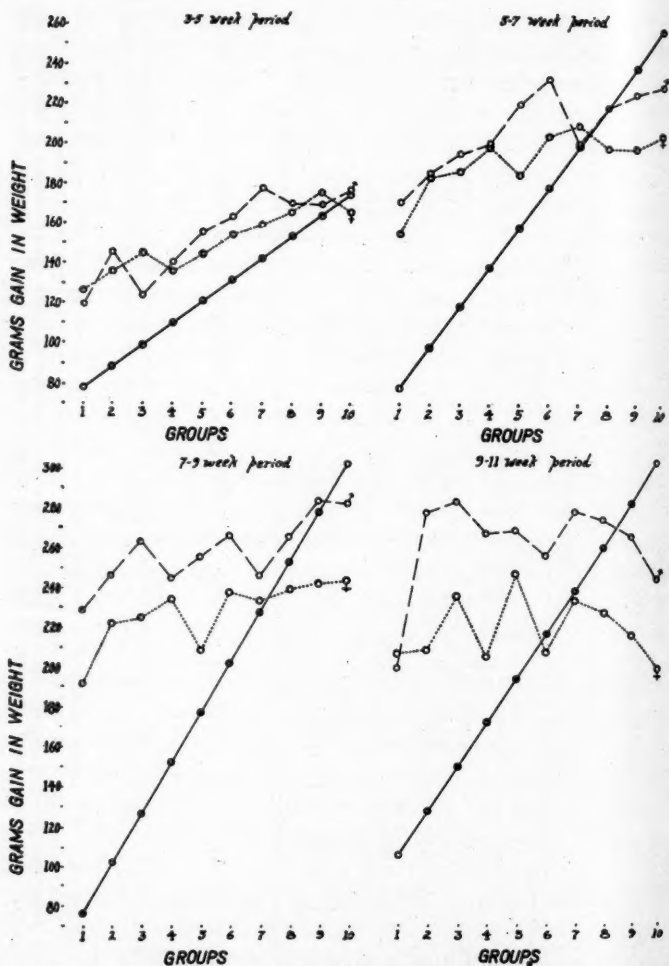
DISCUSSION OF RESULTS

For the entire eight-week period 40 chicks fed a mixture selected by the fastest-growing individuals grew to a weight, on the average, 164.3 grams greater (23.4 per cent. larger) than that for the average of an equal number of chicks fed on the mixture selected by the slowest growers. The results are given in Table V and in Figs. 3, 4, 5 and 6.

That a ration chosen by fast-growing individuals will stimulate unselected chicks to grow faster than will a ration selected by slow-growing individuals can be recognized by the trends of the growth curves.

Fast growth rate in the chick is, then, definitely related to the choice of food: In part it is an expression of an ability to choose foods wisely.

fastest-growing groups as given in Table V supply the information from which all 40 mixed rations used in the proof test may be calculated—by dividing the difference between the two rations given above into 9 equal intervals.



FIGS. 3, 4, 5 and 6. The relation between gain in weight and selection of food. The solid line represents ten different rates of growth calculated from the regression lines for rate of growth from data on 100 Rhode Island Red chicks permitted free selection of food (see Table V). The broken line, representing the males, and the dotted line, representing the females, indicate the actual growth rate of 400 chicks fed ten different mixtures of the food selected by those permitted free choice of food.

Chicks fed mixtures selected by fast-growing individuals grew faster than the chicks fed mixtures selected by slow-growing individuals.

An examination of each two-week period shows that the rate of growth of each group fed mixtures of foods corresponds fairly closely to the trend in growth rate of those who selected the foods. The trends are definite and fairly consistent for 3-5, 5-7 and 7-9 week periods. During the period from 9 to 11 weeks, however, the chicks fed on slow-growth-producing rations tended to grow faster than usual. In other words, those chicks fed fast-growth-producing rations were forced earlier in life to grow at a pace which they could not maintain, while those fed on slow-growth-producing rations continued their growing period for a longer time than usual.

It is well known that certain bodily functions may be modified to increase markedly at the desired time or age, but that this increase is usually followed by a decrease at a later age. The foregoing results show that the time factor must be considered in judging the value of growth as of such other functions as milk secretion and egg production.

It will be noted in Figs. 3, 4, 5 and 6 that chicks fed a mixture of the rations selected by *slow-growing* individuals grew *faster* than those who selected the food, and that, obversely, those chicks fed a mixture of the rations selected by *fast-growing* individuals grew *slower* than those who selected the food. These expressions of a regression toward the mean rate of growth are to be expected, since growth is not controlled entirely by the quality of the food consumed. Not only is there compensation by means of a qualitative absorption of food from the digestive tract, but there are also other means of adjustment to qualitative differences in foods—the most im-

Those fed mixtures selected by fast-growing individuals gained in weight for the four two-week periods +38.9, +33.9, +24.6, +8.5 per cent. more than those fed mixtures selected by slow-growing individuals. The accumulated total gain for the four two-week periods for the chicks consuming rations selected by fast-growing individuals was +105.9 per cent. more than the gain for the chicks consuming rations selected by slow-growing individuals. These differences in growth rate are due to differences in ratios of foods and (except possibly for the last period) are statistically significant.

portant of these being perhaps an adjustment through quantitative consumption.

In Fig. 10 and Table VIII the amount of food required for each unit gain in weight is given for all groups in the experiment. An attempt on the part of chicks (especially those fed mixtures of foods selected by slow growers) to adjust themselves to rations deficient in the nutrients demanded by their genotypes (average genotypes as they are) is shown by the tendency of those consuming slow growth-promoting rations to consume relatively larger quantities of food per unit gain (3.96 grams of food for each gram of gain in weight, group 1) than did those on fast growth-promoting rations (3.42 grams of food for each gram of gain in weight, group 7). Furthermore, when a comparison is made between chicks permitted a free selection of foods and those fed the mixture indicated by this free selection, the slow growers selecting their own foods required 23.5 per cent. more food for the same gain in weight than did those who were required to consume the same ratios of foods. Groups 4 to 8 required approximately the same amount of food for each unit gain in weight, regardless of the mode of feeding—free choice or mixed. But groups 9 and 10, the two fastest-growing groups among those permitted free selection of foods, required less food per unit gain in weight than did those who were fed mixtures of the same foods.

In other words, the foods selected by *slow*-growing individuals when mixed were used *more efficiently* by the average genotype (4.89 against 3.96)—a fact which indicates the presence of genetic factors controlling the efficient utilization of nutrients; and, on the other hand, the foods selected by *fast*-growing individuals when mixed were used *less efficiently* by the average genotype (3.35 against 3.61)—a fact which indicates that these foods adaptable to a superior rate of growth are wasted in part when fed to average individuals.

Separation of the genetic from the nutritional factors related to growth rate are again shown by the relative

influence of sex upon growth and the ability to control these sex differences by alterations in the ratios of foods (Figs. 3, 4, 5 and 6). When identical food mixtures were fed to the two sexes, the growth rate of the males averaged higher than that of the females 35 out of 40 times. As age advanced, the male rate exceeded the female rate more widely. But alterations in the ratios of foods made it possible to force females to grow faster than males, especially during the two periods 3 to 5, and 5 to 7 weeks. During the 3 to 5 week period, group 1 males grew at a rate of 119.3 ± 6.36 grams, while group 10 females gained 165.5 ± 6.33 grams. Comparative data with probable errors are given for the other groups in Table V.

These facts demonstrate that genetic factors responsible for growth rate are expressed in part through efficiency in the utilization of foods and in part through a quantitative adjustment. Furthermore, they demonstrate that genetic factors which dominate other genetic factors under a similar nutrient environment may be submerg'd and even reversed in dominance by alterations in the ratios of foods consumed. Thus the ratios of foods consumed are not alone responsible for individual differences in growth. Genetic factors expressed through quantitative adjustments in the consumption of food and through efficiency in the utilization of food enter into the end-result—growth rate.

The individuality which is expressed by qualitative selection of and quantitative adjustment to foods and by efficiency in the utilization of food is modified by other factors, many of which are non-genetic. In fact, individuality so expressed may actually be hidden among other factors entering into such variations (as indicated in the introduction). All such possible modifying factors, both genetic and non-genetic, must be considered and analyzed before each can be given its appropriate weight in the final analysis of the nature of the nutritive instincts.

The exact part played by all factors which govern individual preferences for food can not as yet be delimited.

Much more experimental work will be required in order to judge the relative value and importance of individual variations. However, the following points are considered pertinent to the problem and are being subjected to active experimentation at the present moment.

A. FACTORS OF A PHYSIOLOGICAL NATURE

(1) *Appetite, hunger and the nutritive instincts.* Adaptive behavior towards agreeable foods and away from disagreeable foods and poisons may be related first to taste,¹² smell and sight, and later to the deeper hidden hunger. It includes both appetite and hunger (Pavlov; Cannon and Washburn; Carlson; Boring; Loeb; and others). It may be concerned not alone with supplying immediate demands and even preparing for future demands (as in hibernation) but also with restoring depleted bodily reserves.¹³

(2) *Alteration of bodily demands with age and with function.* Each age cycle of growth and development and each functional activity has its own food requirements which must be met either from stored reserves or from

¹² In these experiments there were observed strong dislikes for certain foods. The most marked of these was an immediate distaste for alfalfa leaf meal. After the first few pecks (an amount that was below the experimental weighing fluctuation) no more alfalfa was ever eaten. Large numbers of chicks were exposed to this food together with other foods for eleven weeks with no record of consumption of alfalfa leaf meal, and yet the product is widely used as an ingredient in mixed rations.

¹³ Green (1925) expressed a similar notion (with reservations) as an explanation for osteophagia in cattle grazing over phosphorus-deficient veld, p. 347: "The simplest explanation is that certain members of a grazing herd, on the verge of allotriophagia, or indiscriminate craving, develop a selective taste for material which happens to be available, and at the same time effective in creating a feeling of well-being; that they learn by experience that certain recognizable available objects offer more relief in the long run than others; and that other cattle imitate the procedure as a 'trick of the herd' but soon discover that it satisfies an instinctive need. An objection to this view is that young cattle brought up in an area carefully cleaned of all bone debris have yet been found to manifest osteophagia the first time bones were displayed before them. It is possible that the cleaning process may not have been perfect, but so far as is known these individuals had no chance of learning the habit, i.e., of profiting by the experience of an osteophagic herd."

food immediately available. Both storage and immediate demand appear purposive in their action.

(3) *Differences in bodily demands between genotypes.* Different genotypes or phenotypes controlling form or function must be closely allied to the ability to choose food wisely. In the same way that one individual is able to alter its choice of food in accordance with the requirements of each stage of its growth or life cycle, so are individuals with differing genetic make-up able to make a selection of food in accordance with their differences in form and function.

(4) *Specific maturation of the abilities to discern food differences.* As stated previously, although experience with the reenforcement of habit may be responsible for some of the variations in choice of food with age, the abilities to choose food wisely appear to go through a maturation period.

(5) *The effect of habits which hinder or prevent the search for new and superior foods.* Habit prevents vacillation from one food or one condition to another. If the habitual food is non-injurious and remains nutritious, survival, at least, is insured. In this respect habit may have survival value. Habits, however, are unadaptive and hinder the selection of new and perhaps superior foods. Once a choice is made for a particular group of foods and once habit has fixed attention on those foods alone, other choices are to a large extent automatically prevented (Harris, 1933). The future development and fate of an individual is thereby tied closely to the food habits developed early in life. Early habit must have an opportunity to stabilize a liking for those varieties of foods which will furnish vitamins, minerals and nutrients necessary for optimum phenotypic expression. Otherwise habit may become a lethal factor.

(6) *Food jags.* Sometimes animals allowed a free choice of food will confine the day's food ration to only one food—as is said, will “go on a food jag.” At times this desire for a particular food is maintained for days,

later to be superseded by a jag on some other food. Davis observed this phenomenon in the infant and considered it unharmed. Both Nevens and Evvard considered it of more harm than value to the animal.

Food jags have been observed in this laboratory to occur frequently in birds, calves and rats, a certain amount of vacillation from one food to another seeming to be the rule. Food jags have been included in the general problem of comparing the feeding of food mixtures with separate feeding of the same foods—a jag being considered as one extreme and a complete mixture of all foods as the opposite extreme. Either extreme in feeding methods may be harmful. The extent of the ability to endure monotonous mixed foods in terms of degree and time has not been completely worked out. It is possible that the monotony of consuming an all-mixed ration may be alleviated by introducing an amount, as yet undetermined, of variation in food from time to time.

(7) *Dissipation in food desires.* When food desires become so extreme as to be abnormal, they may be labelled dissipations. Some food dissipations, pathological in form, are related directly to improper functioning of some organic system. These may be recognized in such general excessive food demands as bulimia, hyperorexia, polyphagia. Other forms of food dissipation begin as relatively harmless food jags, but strengthened by habit may induce pathological conditions. Examples are such specialized abnormal demands as are exhibited in alcoholism and addictions to drugs and sugar.

(8) *Social interactions affecting food choice.* The human being and the gregarious animal are strongly influenced in their choice of food by social factors. Racial and religious customs have often been responsible for the color, variety and even quantity of foods consumed by the various peoples of the world. Human beings and animals alike are influenced in food choice by economic and social compulsion, by competition for food and by imitation and suggestion. Education, also, has helped to

stamp upon the people and the live stock the nutritional notions of the times.

B. FACTORS OF AN ACCIDENTAL NATURE

Foods which the individual senses first may, through associations, become especially favored or disfavored. Chance would thereby be considered a factor responsible for some of the individual variations in the choice of food. Chance associates also influence choice of foods. Most important of the factors of chance are those which affect the availability of foods and the nature of the foods available.

The relative abundance and variety of foods to which a group of individuals have access obviously serve as natural selective agents in survival. Furthermore, the foods available not only assist or deter survival but also significantly alter the individual expression of the surviving type. The effect of availability of foods is recognized in the characteristic food habits of the different races of the world and in the different methods of rationing animals upon the products of local geographical areas. Furthermore, alterations in the nature of the foods available, either through variety changes or through loss of soil fertility or drouth, etc., are directly associated with the deficiency diseases of the consuming animal or man. The availability of foods and the nature of the foods available, then, form an important phase of food selection studies. This subject will be discussed in greater detail in a subsequent section.

Even in face of the power of modifying factors to alter or to duplicate the expression of the genetic impulse toward food choice, there nevertheless remains a certain indomitable consistency in the proportions of each food combination selected when as many as possible of the modifying factors are kept constant or are partialled out statistically.

The forty groups of chicks showed a well-defined consistency of food preference (Table VI and Fig. 7). For

TABLE VI
CONSISTENCY IN THE CHOICE OF FOODS*
(In parts per hundred)

Foods	3-5 weeks		5-7 weeks		7-9 weeks		9-11 weeks	
	Mean P.E.m	C.V.	Mean P.E.m	C.V.	Mean P.E.m	C.V.	Mean P.E.m	C.V.
Corn meal	55.40 ± .78	13.2	54.35 ± .78	13.5	58.35 ± .84	13.5	58.93 ± .86	13.7
Fish meal	7.20 ± .29	38.3	8.43 ± .33	37.1	8.80 ± .38	40.5	10.17 ± .42	39.1
Bone meal	1.00 ± .09	83.7	2.90 ± .18	58.3	4.00 ± .25	57.5	4.53 ± .30	62.7
Oyster shell flour28 ± .05	162.4	1.03 ± .03	25.3	1.00 ± .08	74.2	1.43 ± .03	22.1
Wheat bran	19.18 ± .60	29.4	17.80 ± .58	30.4	13.27 ± .60	42.3	12.10 ± .58	44.8
Skim milk powder83 ± .15	175.4	1.15 ± .17	135.7	1.43 ± .15	101.4	1.70 ± .18	97.6
Oat meal	13.33 ± .72	50.9	11.30 ± .77	64.0	10.10 ± .58	53.5	7.97 ± .49	57.2
Food constituents								
Protein	15.31		15.90		15.90		16.38	
Ca61		1.35		1.59		1.91	
P75		.96		1.03		1.10	

* Records based on 400 Rhode Island Red chicks (started). Each group average is considered as a single item. n = 40.

instance, corn is the food most desired by every group. Each food was selected with a characteristic limit and range of choice, even though the individuals which made up different groups were selected differently for gain in weight and even though gain in weight is correlated with choice of food. In other words, the figures in Table VI are perhaps more extreme in variation than would be found in a similar series of unselected individuals. The inter-group range in choice of different foods is shown graphically (Fig. 7).

The foregoing ratios of food consumption hold true only for the particular combination of foods. The exchange of any one food for a new food usually alters the ratios consumed of those foods common to both series. Thus the animal is able instinctively to adjust itself to the complementary action of foods—an interaction which has so far remained beyond biochemical appraisal.

Résumé: Survival in the past has depended upon the nature of the choice of food. Whatever means may have existed for the detection of foods of value to survival have continued to protect the species and guide its food choices in an apparently all-wise fashion. However, as we have shown, the instincts themselves are not always wise, *i.e.*, are not always functioning to produce optimum results or are over-functioning and out of balance with other factors concerned in nutrition. In the chick this ability to select the proper food is present to some extent at emergence from the shell, but not until after the first few weeks of life, during which the absorbed maternal yolk supplies an important part of the nourishment and the chick passes through a period of maturation or learning, is the chick thrown upon its own ingenuity in the choice of food. In mammals the lacteal secretions produce a fairly completely balanced (all-mixed) food for the young during its maturation or learning period, but milk, even though popularly considered the perfect food, can not alone support normal life for more than a few months and, under natural conditions, must serve merely

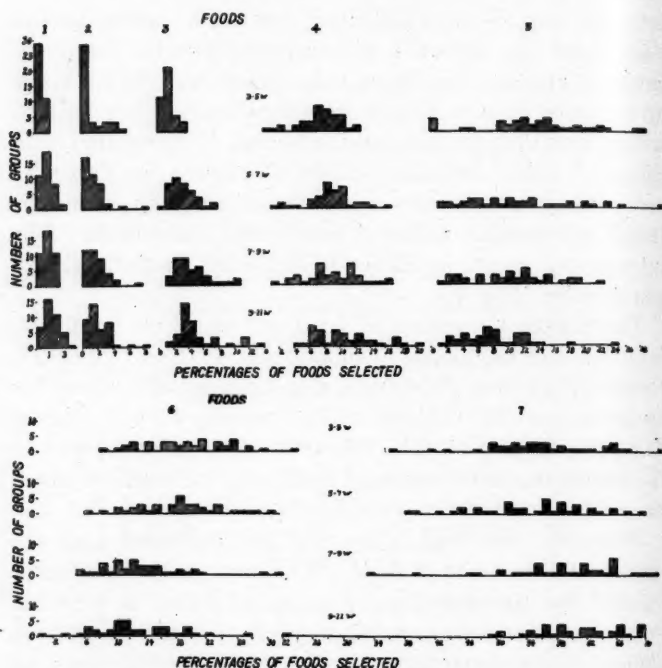


FIG. 7. The proportions of foods selected free-choice by forty different groups of chicks during four different periods of growth from 3 to 11 weeks of age. Each food was selected with a characteristic frequency with well-defined limits of variation, even though the groups were selected and re-grouped at the end of each two-week period in serial order according to gain in weight. The foods are numbered as follows: 1=Oyster Shell Flour; 2=Dried Skim Milk Powder; 3=Bone Meal; 4=Fish Meal; 5=Oat Meal; 6=Wheat Bran; 7=Yellow Attrition Corn Meal.

as the transitional food supply to bridge the gap in life from the time when maternal blood ceases to supply all the nutrients up to the time when the maturation of the instincts and the gain in experience make it possible for the animal to choose food. After the maternal supply of egg yolk or milk is exhausted, the young is dependent on its own native instincts (or those of its associates) for survival. Obviously those individual genetic variations in the nutritive instincts which are successful are

taken over by the surviving genotype in the process of evolution. Thus individuality in the nutritive instincts should be recognized as equally important with any other character of survival value.

Our experimental results, then, point to the following conclusions: That natural selection has brought about the survival of those animals possessing to a high degree the abilities to judge food from non-food and to select the proportions of foods required for survival in an apparently purposive fashion. That these abilities may be termed, as a group, the nutritive instincts. That there are marked differences in the abilities of individuals to choose food wisely. That the superior choose foods which supply the nutrients for that superiority and in so doing are wise. That the inferior or unwise, on the contrary, are left behind in the class of physically deficient or are immediately eliminated. That a number of factors bring about results similar to the results of wisdom and unwisdom. That some of these factors are entirely non-genetic. In short, that natural selection works both upon innate individual differences and upon those extraneous factors which remain throughout successive generations as consistent elements of the nutritional environment to produce the characteristic forms and functions of the surviving type.

VARIOUS INFERENCES DERIVED FROM THE RECOGNITION OF INDIVIDUALITY IN THE NUTRITIVE INSTINCTS

The second section of this paper deals with various inferences derived from the foregoing experiments and considers, with new experimental data, the concept of individuality which is expressed in the nutritive instincts as it enters into the complex network of interaction between heredity, instincts, nutrition and society. It also considers the extent to which the behavior recognized in the nutritive instincts may be typical and useful in the analysis of "purposive" or directive behavior in general.

RELATION BETWEEN GENETIC AND NUTRITIONAL
FACTORS FOR GROWTH

In so far as either instinctive or acquired desires for certain foods may be the guide to the foods which are needed, the important application of these experiments lies in the fact that choice of foods may be used to formulate that ration which will produce a type of individual like that which does the choosing. Evidently, to a certain extent,¹⁴ the superior individual is able to recognize the ratios or combinations of foods which he should consume.

It is not implied that superiority is necessarily associated with increased rate of growth (although, as far as growth as a character in itself is concerned, such an association is valid). It may be found that other elements involved in general superiority will be incompatible with a fast rate of growth. It can be shown, for example, that neither a slow nor a fast growth rate is always compatible with longevity. McCay has recently (1933) stated that slow growth rate is more compatible with long life than is fast growth rate in rats fed a mixed ration. But during the course of these experiments evidence continually pointed toward a harmful effect of both excessive and retarded growth rate when animals were allowed free choice of their food. The highest death rates occurred among those which grew either too slowly or too rapidly. A value somewhere between the mean and the maximum appears to be the value of the superior surviving class.

When consideration was given to the individual differences in food choice associated with fast rate of growth, there was observed a certain general trend from group to group either for or against a certain food as growth rate increased. Increase in growth rate was usually associated with an increase in the relative consumption of corn. The regression lines secured from

¹⁴ The association between superiority as expressed in growth and wisdom in the choice of food though statistically significant nevertheless does not permit a simple statement of fact. The exact degree of wisdom inherent in the most superior individual has not as yet been determined.

duplicate and repeated trials, however, do not always coincide. In Fig. 8 are shown the four regression lines both of corn and of dried milk consumption against gain in weight from four repeated experiments (100 individuals per trial). The regression lines show that while

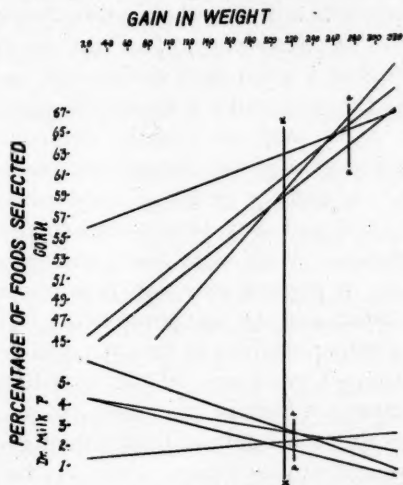


FIG. 8. The relation between gain in weight and food selection. The regression lines indicate the consistency in choice of food with gain as made by four different groups of Rhode Island Red chicks, 100 chicks per group. \bar{x} — \bar{x} = mean growth rate for all four groups as 211.46 ± 3.55 grams. a — a = growth rate where the four groups are in closest agreement among each other, i.e., where the sum of the deviations from the means is the least. When the combined a — a value is calculated for all seven foods accessible to a free selection, the point of agreement is found to lie between the mean and the maximum growth rate, a rate which has been here considered as the optimum rate of growth for the foods and the genotype concerned.

the proportions of the food consumed by all the groups ranged closely about a nucleus common to each food—corn consumption varied from 49 to 69 per cent. and dried milk consumption varied from .5 to .8 per cent. (see Fig. 7), yet a variable relation existed between gain in weight and the rate of consumption of each food and that these values varied with each repeated experiment. This latter form of variability reached an extreme when

increased gain in weight might in one trial be associated with *more* of the particular food, and in another trial with *less* relative consumption of the same food. On the surface it appears that never twice are the conditions so alike as to produce similar results. However, a closer examination of this problem will reveal an interesting consistency within the lack of consistency. In Fig. 8 all four regression lines cross at a point near each other, *i.e.*, at a gain of 275 grams for corn and a gain of 220 grams for dried milk. This point may be exactly determined as the point where the sum of the deviations from the means is the least. A similar point of concordance may be observed to exist and may be determined for each food in the experiment. With some foods the value falls outside the range of growth rate, but it is generally found between the mean and the maximum rate of growth.

A working interpretation of this phenomenon rests on the recognition of wisdom (in the nutritive instincts) as a phenomenon which is universal but is capable of expression as universal only at that rate of growth where the two classes of unwise (those which err on the side of insufficiency and those which go to excess) equally balance each other, only at that point where the expression of the group is equal to the expression of those individuals which are securing the correct ratios of foods for the optimum expression of their genetic potentialities.

The individuals which failed to consume the correct ratios of foods and failed thereby to gain 275 grams in weight for the two-week period, differed from trial to trial in their judgment, we might say, as to choice of food (corn). The amounts of foods consumed are as a consequence highly variable. Furthermore, with those individuals which grew exceedingly fast (more than 275 grams in two weeks, in this instance), there was a tendency to disagree (between groups) as to what foods to consume for fast growth, and, even though they consumed different amounts of food than did those which gained slowly, and fluctuated in desires on an entirely different

level of food consumption, yet they vacillated from trial to trial in the same manner described for the slow-growing individuals. However, the wise individuals, those which grew neither too rapidly nor too slowly for their phenotype, are found to grow at that rate where the number of individuals which go to excess counterbalance the number which fail to secure a sufficient food supply for their phenotype. At this point of concordance we find what will be termed the point of *optimum gene-nutrient combination*.

If this point were secured from data on a single food, our recognition of it could not be justified. Calculations must be made upon a composite of the data secured on all of the foods used in the experiments. The average value of them all should indicate more nearly the actual ratios of foods required for the optimum growth rate as indicated by the composite of reactions attributed to the nutritive instincts as they combine with the assortment of foods made available to the particular genotype.

Calculations have been made on the records secured from these four repetition experiments to determine for each two-week period by the method indicated in the preceding paragraph the optimum rate of growth. In each instance the optimum appears as a value higher than the mean, although never as high as the maximum. (See Fig. 9.) The optimum growth rate of all four two-week periods exceeds the mean growth rate by an average of 71.1 per cent. of the standard deviations. In other words, in these experiments the optimum rate of growth is not that of the fastest-growing individual, nor of the average, but is equal to the rate of growth of the individual which gains at a rate higher than that of approximately three fourths of the population.

From this figure we are able to calculate the optimum rate of gain for each two-week period as well as the proportions of foods required to make that particular gain in weight possible. These figures are given in Table VII. A study of these figures reveals a remarkably consistent trend from period to period of the growth cycle.

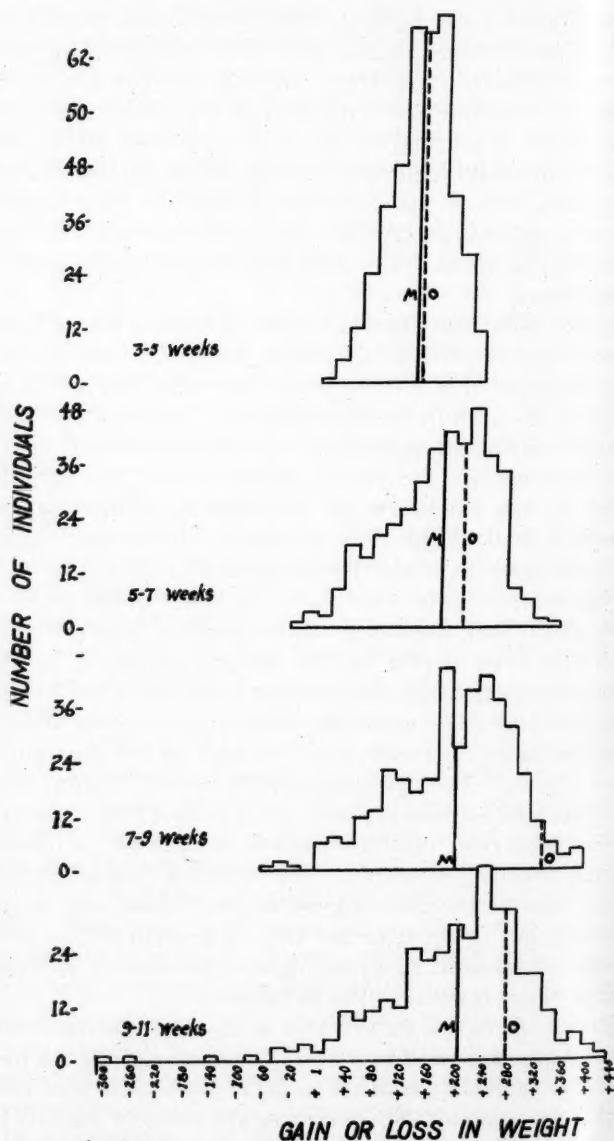


FIG. 9. Optimum gain in weight during each two-week period. O = optimum rate of gain in weight, determined as the point (gain) at which four

TABLE VII
CALCULATED RATIOS AND CHEMICAL COMPOSITION OF FOODS SELECTED FOR THE
AVERAGE OPTIMUM RATE OF GROWTH

$$\left(\frac{\sigma}{.711}\right)$$

Foods	3-5 w. 172.67 gr.	5-7 w. 230.57 gr.	7-9 w. 265.21 gr.	9-11 w. = Weeks of age 284.42 gr. = Average optimum gain
Corn meal ...	55.52%	59.60%	64.07%	65.38%
Fish meal ...	9.12	11.53	11.41	11.89
Bone meal ...	1.32	2.99	3.50	4.23
Oyster shell flour86	1.26	1.25	1.60
Wheat bran	19.47	17.86	12.23	11.34
Skim milk powder81	.85	1.77	1.17
Oat meal	12.90	5.92	5.77	4.38
Food constituents				
Protein	16.42	17.13	16.97	16.96
Fiber	3.68	3.31	2.85	2.73
N.F.E.	58.29	56.02	56.18	55.80
Fat	5.54	5.69	5.57	5.59
Salt50	.63	.62	.65
Lactose40	.42	.88	.58
Ash	5.59	7.26	7.34	8.12
Calcium96	1.55	1.66	1.96
Phosphorus	.83	1.02	1.02	1.09

Further substantiation of the fact that the optimum rate of growth lies between the mean and the maximum value is secured from a comparison between the gain in weight made by the chicks fed free-choice with the gain in weight made by the chicks in the check experiments, who were fed the indicated mixtures of the same foods

different groups of chicks (100 individuals per group) were in closest agreement as to the choice of food. The optimum O has been calculated as an average from the 4 regression lines for all seven foods. M = mean gain in weight made by the same 400 individuals. The optimum gain in weight falls between the mean and the maximum rate of gain in all four growth periods. The optimum of the four periods averages 71.1 per cent. of the σ on the positive side of the mean.

(Figs. 3, 4, 5 and 6). The highest average gain made by any such check group totaled for the 8 weeks 865 grams. This gain in weight is 21 grams more than the average gain of 844 grams made by those permitted a free choice of food—a value which lies between the mean and the maximum.

The amount of food required per unit of gain in weight varied with growth rate (Fig. 10). A slow rate

TABLE VIII
GRAMS OF FOOD REQUIRED FOR EACH GRAM OF GAIN IN WEIGHT

Group	On free choice*	On ration mixed* according to free choice
1 (= Slowest growth rate)	4.89 grams	3.99 grams
2	3.95	3.63
3	3.83	3.50
4	3.72	3.61
5	3.51	3.53
6	3.61	3.51
7	3.50	3.42
8	3.47	3.47
9	3.31	3.48
10 (= Fastest growth rate)	3.35	3.57

* Records based on 400 Rhode Island Red chicks (at start).

of growth required definitely larger amounts of food—as would be expected from energy calculations—than did a fast growth rate. The chicks to which the series of mixed foods was fed varied in their efficiency in the use of the food in a fairly consistent trend away from the inefficiency of both the slow- and the fast-growing individuals toward that height of efficiency characteristic of group 7—a value midway between the mean and the maximum.

That both too rapid and too slow a rate of growth are the signs of failure to secure the proper nourishment is also shown by the higher incidence of mortality among the individuals characterized by either fast or slow

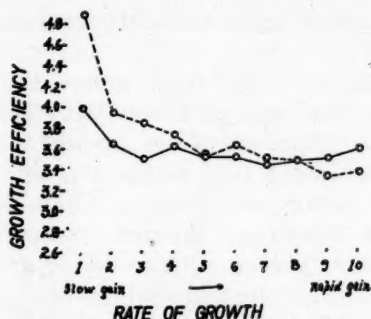


FIG. 10. The quantity of food required for each unit gain in weight. 0----0 = data from 400 chicks permitted a free selection of food from 3 to 11 weeks of age. 0——0 = data on 400 chicks required to consume mixtures of foods selected by the former groups. *Growth Efficiency* = grams of food required to produce one gram increase in live weight. *Rate of Growth* = the result of sorting of chicks on free choice into ten groups ranked serially according to average gain in weight: group 1 contains the slowest-growing and group 10 the fastest-growing individuals. Those fed the mixed ration (solid line) were distributed so that all groups were alike genetically in their ability to utilize food efficiently. The ratios of foods which they were required to consume altered the expression of their genetic ability. Of these chicks group 7, a group which grew at a rate between the mean and the maximum, made the best use of the mixed ration.

growth rate. This point will be taken up in greater detail in a subsequent section.

Evidence from four different sources, then, points toward the fact that an optimum rate of growth exists somewhere between the minimum and the maximum. Three of these sources¹⁵ definitely place that optimum at a point between the maximum and the mean, at about .7 to .8. These facts include: High variability in choice of foods made by those growing extremely fast and extremely slowly; a close agreement on proportions of foods which produced a rate of growth as stated; an increased efficiency in the use of mixed foods reaching its highest value with a growth rate .7 of the maximum;

¹⁵ The fourth source of evidence for localizing the optimum rate of growth is longevity records. Until the experiment is terminated and data secured on the length of life of all individuals in the experiment, the optimum rate of growth in relation to longevity can not be more closely delimited than as stated above.

and the existence of higher mortality rates among extreme individuals.¹⁶

Experimental evidence, then, proves the thesis propounded at the beginning of this section: That by following the nutritive demands of the superior individual, one may be able to inject a part of that superiority, in so far as nutritional factors contribute to it, into the individual which would otherwise, through extraneous circumstances, be only average. By so doing, one may bring out the maximum genetic potentialities of individuals who otherwise would dally around a mediocrity due to environmental (including social) limitations.¹⁷ By exposing groups of individuals to rations mixed according to a graded series in terms of effect upon growth rate, one may readily determine the maximum rate of growth compatible with longevity or with any other trait desired.

¹⁶ With this information at hand we must conclude that the free-choice method of feeding children recommended by Davis can not be relied upon as adaptable to *all* children. Some (if the human being's reaction is similar to that of experimental animals) will consume foods in excess and others will fail to secure the elements for optimum nutrition. Experimental animals on free-choice experiments vary more highly in their gain in weight than do those individuals required to feed on mixed rations. Some of the slowest and some of the fastest-growing individuals are found among the free choosers, while those on mixed rations show more inter-individual consistency in their growth rates. This fact is shown in Fig. 11, which represents the gain in weight from 3 to 11 weeks made by the two groups (381 individuals each per group finished the experiment), one group on free choice of food and the other fed the ten different mixtures of the same foods. Even though the ten different mixtures of foods represented rations producing ten different rates of growth and included both slow and fast growth-producing rations, nevertheless the frequency distribution of those on mixed rations shows less variability (C.V. of 24.3 per cent.) than that of those on a free selection of food (C.V. of 30.5 per cent.).

	n	Mean gain	P.E. _m	σ	C.V.
On mixed rations..	381	835 \pm 6.3	191	24.3 per cent.	
On free selection of food	381	844 \pm 8.4	242	30.5 per cent.	

¹⁷ Although we are here concerned with bringing out the maximum expression of the genotype, we question the advisability of inflating the phenotypic expression above the optimum expression controlled by genetic factors.

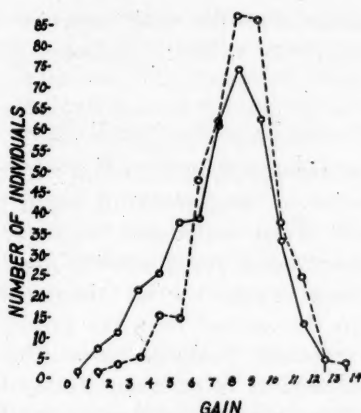


FIG. 11. Comparison between free selection of food and mixtures of foods as expressed by individual gain in live weight from 3 to 11 weeks of age (Rhode Island Red chicks). 0——0 = on free selection; 0---0 = on mixed rations.

This method is an application of nature's best method of rationing, a method which may or may not prove to be superior to the modern scientific methods of rationing. Death of the grossly unwise has guaranteed through both natural and artificial selection the survival of a type of individual which would inherit the ability to make the proper choice of foods. No such incentive has been present to prod the nutritionist toward the formulation of a complete ration for animals. And as for man himself, he still relies largely upon these same nutritive instincts.

However, in those animals which could safely depend upon their ability to choose food for superior function or form, numerous extraneous forces interfere with and hinder optimum opportunity for the expression of this ability. Thus, if only two different foods are available, the wisest individual may not grow as fast as the least wise in a group having access to six different foods. (See Table XII.) These limitations in opportunity and other modifying factors previously mentioned affect and modify the results secured from individual choice of food.

For these reasons even the most superior may fail to express completely its ultimate optimum genetic potentiality.

RELATION BETWEEN RAPID GROWTH RATE AND LONGEVITY

McCay has stated (1933, p. 411) that "no one has ever found it possible . . . to have both rapid growth with early attainment of maturity, and longevity. It is possible that longevity and rapid growth are incompatible and that the best chance for an abnormally long life span belongs to the animal that has grown slowly and attained a late maturity." On the basis of his own experiments and of historical references, McCay has attacked the principle behind the present-day wholesale feeding of growth-promoting adjuvants to the human race (McCay and Crowell, 1934).

In the preceding section the writer has drawn the conclusion that on the average not only the excessively fast but also the excessively slow rate of growth are incompatible with longevity. It will be noted that our conclusion was based on the adoption of a free-choice method of feeding. The experiments reported by McCay, showing that slow rate of growth is more favorable to long life than fast rate of growth, were made on mixed rations. The writer feels that any real test must be made on a free choice of foods, since obviously any scientifically mixed ration can not be universally adapted to all rates of growth and conditions of life but will be over-balanced or out of balance in some one respect for the individual as such or for a particular period of life or of bodily function.

We may clarify our principle by pointing to the well-known harmful effect of forced feeding on animals and of forced commercial fertilization on plants,¹⁸ both of

¹⁸ In the days of the early New England settlements, fish were used extensively as a soil fertilizer. The high nitrogen and phosphorus content stimulated crop production in a striking manner. But after a few years of abundant harvests the crops lodged and decreased in yield because of a depletion of the available soil potassium and a lack of potassium in the

which practices commonly make no allowance for the tax exerted by rapid growth and excessive cropping on trace minerals. With the free choice of foods the difficulties are partly eliminated, since the individual is free to secure a balance of all ingredients required for fast rate of growth (provided that all of them are available for selection). According to the recognition of individual differences in the ability to choose foods wisely, we should expect some of the fast-growing individuals to be able to select foods conducive both to fast rate of growth and to long life.

In 1933 one hundred chicks were started, at 3 weeks of age, upon experiment with six foods from which to choose. For nearly two years their only means of subsistence has been these same six foods. The growth data have been ranked according to the rate made during the period from 5 weeks to 21 weeks of age,¹⁰ and these figures

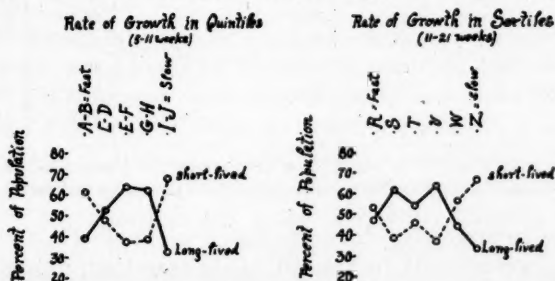


FIG. 12. Relation between growth rate and longevity. The majority of both fast- and slow-growing individuals are short-lived. Nevertheless, some individuals are able to select food which permits fast rate of growth without shortening life.

fertilizer added. Settlers were warned against this practice of "herring the soil."

In a similar manner forced growth is commonly recognized by the nutritionist as ill-advised in the long run. He recognizes that the largest and fastest-growing infants and experimental animals are the first to show the clinical signs of deficiency diseases, especially rickets. The heaviest milk producers among dairy cattle are usually the first to show signs of nutritional deficiency diseases.

¹⁰ Five weeks was used as the beginning of calculations since 3 to 5 weeks was the first period of growth during which a free selection of food was permitted.

have been compared with the mortality rates. (Only females are considered here; most of the males were removed from the experiment at 8 months of age.)

TABLE IX
RELATION BETWEEN GROWTH RATE AND LONGEVITY (WHEN FOOD IS
PRESENTED FOR FREE SELECTION)

Growth during three 2-week periods (from 5 to 11 weeks of age)			Growth during five 2-week periods (from 11 to 21 weeks of age)		
Growth rate in quintiles	Female birds dying before 1 year of age	Female birds alive at 1 year of age	Growth rate in sextiles	Female birds dying before 1 year of age	Female birds alive at 1 year of age
Number of 2-week periods =	78	60		116	99
Fastest = A B	60.4%*	39.6%*	R = Fastest	53.1%*	46.9%*
C D	48.0	52.0	S	39.1	60.9
E F	37.4	62.6	T	46.0	54.0
G H	38.5	61.5	U	37.5	62.5
Slowest = I J	67.9	32.1	W	56.6	43.4
			Z = Slowest	66.9	33.1

* The actual figures on which these percentages are based were first corrected to equal a total of 100 individuals for both the living and the dead.

The comparative data are listed in Table IX and are shown graphically in Fig. 10. It is seen that, in general, both fast and slow rate of growth are incompatible with long life, but that nevertheless from 39 to 46 per cent. of the fast growers belong to the relatively small group now living. Therefore *some individuals* are able to select foods which produce fast rate of growth and still to be classed among the long-lived.

A METHOD FOR ANALYZING THE CAUSES OF NUTRITIONAL DEFICIENCY DISEASES IN ANIMALS AND MAN

Since some individuals are wise and others are unwise in their choice of food, the opportunity is given through an analysis of the rations consumed by individuals with iden-

tical deficiencies to determine by biochemical methods the cause of such deficiencies. Individuals which do not consume sufficient quantities of yellow corn, for instance, tend to show the symptoms of vitamin A deficiency, and those which fail to consume sufficient quantities of the mineral or vitamin D carrying foods show rachitic symptoms.²⁰ By observing a group allowed free access to a limited choice of food, one is able to detect and pick out individuals showing many of the commonly recognized symptoms of deficiency diseases known to be due to a lack of the proper mineral or vitamin balance and, through a study of the foods which they have selected, to recognize a direct correlation between certain foods and certain bodily defects. Likewise it is possible, with this recognition of individuality, to discover by the same method of food analysis the causes for defects in bodily form or deficiencies in function which have heretofore been unresolved.

Throughout the numerous preliminary trials in which a search was being made for the proper assortment of foods required for normal development, many new defects appeared. These defects would sometimes occur in a large proportion of a group, would show specific characteristics, would appear at definite age levels and would occasionally occur in one sex more frequently than in the other. Thus, in one experiment, a creeping condition developed during the third week. During the third to the fifth week a large proportion of the individuals was afflicted with this defect. Later the condition disappeared. At 13 weeks of age a condition somewhat similar occurred, particularly among the males. From the thir-

²⁰ Numerous forms of perverted appetites—such as pica; wool, hair and feather eating; coprophagia; infantophagia; egg-eating; salt-hunger, etc.—have been considered nutritional deficiencies. The occurrence of osteophagia (bone chewing) has been traced to a lack of phosphorus (Green, 1925). The simple observation was made that the afflicted have a great predilection for bones and that the severity of the deficiency may be judged by the height of the craving for bones. Subsequent tests on the addition of phosphorus to the ration identified the missing element toward which the nutritive instincts directed.

teenth to the nineteenth week many of the males so afflicted succumbed while the females, scarcely affected, survived.

A correction for these deficiencies was found by a study of the food desires of the superior individuals in contrast to those of the inferior. There was found, for instance, a definite correlation between the consumption of wheat middlings and the failure to gain weight rapidly, as Table X shows.

TABLE X
ASSOCIATION BETWEEN GAIN IN WEIGHT AND DISLIKE FOR CERTAIN FOODS
(Periods from 7 to 9 weeks of age, Groups 261-270, 1933)

Rank in order of increasing gain in live weight	Gain in weight based upon average of 10 individuals	Per cent. that wheat middling flour formed of the entire ration
1	167.6 grams	21.52%
2	211.3	22.94
3	231.1	12.50
4	255.5	16.34
5	269.1	7.96
6	279.1	4.26
7	281.0	5.60
8	313.5	4.89
9	319.7	4.38
10	329.9	1.55

The foregoing record is representative of numerous experiments in which wheat middlings was presented with wheat bran and oat meal for free selection.²¹ Furthermore, this result coincides with the decrease in rate of middlings consumption which accompanied the increase of the abilities (through maturation or learning) to choose food wisely. (See Fig. 1.) The records indicate that wheat middlings supplies nothing of advantage (unless the retarding effect of this food on growth rate should prove, as it may, to be advantageous to long life). When wheat middlings was replaced by dried skim-milk powder,

²¹ Wheat middlings loses preference when wheat bran and oat meal are also available for free selection. When wheat bran and oat meal are absent, wheat middlings increases in preferential value.

very small percentages of this milk powder—generally less than an average of 2 per cent.—were consumed, but even the smallest amounts prevented those deficiencies which had occurred from 3 to 5 and from 13 to 19 weeks of age.

The interrelation between food choice and deficiency diseases is even more clearly indicated in the following check test on the deficiencies evidenced by this creeping condition. As we have stated, the symptoms were at a height during the third to the fifth week of life. They were found to be corrected in a large proportion of the individuals by making available for free choice small amounts of dried skim milk before three weeks of age. In one test a group of 100 were allowed free choice of the same foods, including dried skim milk. Whenever cases of this deficiency "creeper" appeared during the third to the fifth week period, the deficient were segregated from the normal and permitted to choose foods by themselves in order to indicate what foods they desired or did not desire. This method had one severe drawback: the fact that food choices were not recorded separately until after the deficiency had appeared, a difficulty which can not be prevented in group feeding. Nevertheless, the results in Table XI show that the deficient birds were

TABLE XI
RELATION BETWEEN DEFICIENCY DISEASE SYMPTOMS AND FOOD SELECTION*

	Corn meal	Fish meal	Bone meal	Oyster shell flour	Wheat bran	Skim milk powder	Oat meal
Food ratios selected by normal birds (3-5 weeks)	64.3%	14.8%	1.6%	1.1%	8.2%	2.7%	7.4%
Food ratios selected by deficient birds (3-5 weeks)...	83.0	6.4	1.5	0.3	5.9	2.9

* Records based upon 100 Rhode Island Red chicks (at start of experiment).

selecting, during manifestation of clinical symptoms, an excess of corn, a deficient amount of fish (the only vitamin D-carrying food in the group), less bran and oats than normal and no dried skim milk.

Thus a study of the food choices made by individuals prior to and concomitant with the appearance of the deficiency diseases should make possible, through an analysis of the factors supplied by the exchange of any two foods, the discovery of the actual causes of new deficiency diseases. Further analysis through appropriate biochemical methods should make possible the detection and isolation of the advitant concerned. Whereas in the past the biochemist has been dependent upon chance occurrence for the discovery and for the interpretation of the causes of such deficiencies, he is now enabled, by enlisting the aid of the nutritive instincts and associated phenomena, to analyze these deficiency diseases as they occur under natural conditions with the causal relationships partly exposed at the time of their occurrence.

In proposing this method of resolving the causes of deficiency diseases experimentally, it is recalled that certain attempts to analyze, from data yielded by surveys, the relation between defects and food habits in the human being at the time of the deficiency have been, for the most part, unsuccessful. In one of the more recent studies, that of Brown (1934), there was found very little correlation between the food habits of children and the nature of physical defects. Failure to find such a relationship in the human being is probably due in part to the inability to secure exact food consumption data over significantly long periods of the life cycle and in part to the drag between the time that the food was deficient and the time that clinical symptoms of the deficiency appeared.²² It should be possible, however, to formulate a system of

²² A direct association between food and deficiency should be detected in those human beings who are subjected to permanent malconditions of the environment (such as the lack of ultra-violet rays in a cloudy country) or to permanent partial deprivation of vitamin-containing foods (as in a non-citrus fruit area).

securing data on the food consumption of the human being, to be taken periodically over a number of years, which would be comparable to the technique adapted here to the laboratory animal.²³

BIOLOGICAL ASSAY BY MEANS OF THE NUTRITIVE INSTINCTS
AND THE FORMULATION OF MIXED RATIONS FOR LIVE STOCK

Frequently in biological assay work the biochemist is called upon to assess the vitamin or nutrient value of some complex food product. To balance the ration containing the new food so as to insure normal growth of the experimental animals is frequently a disturbing problem. For instance, even with painstaking corrections for differences in energy and in the principal minerals which the proteins contain, the substitution of one protein for another will not always produce normal growth in the experimental animals. This failure to secure normal growth is obviously due to a failure on the part of the experimenter to balance all the hidden factors brought out by the interaction of foods.

But if these same foods are fed free-choice, some individuals will be able to grow normally, and a notation of their food desires will make possible the formulation of

²³ Although a number of factors would interfere with a clear interpretation, the application of such a technique to the problem of deficiency diseases and food habits in man has some very interesting possibilities. If we knew, for instance, what foods have been selected during the entire lifetime of different physical and mental types—by the wrestler versus the philosopher, the mechanic versus the musician, etc., to the extent that nutrition entered into their art or science (in its effect on temperament and on the release of both mental and physical energy) we should have in our hands valuable methods for developing suitable food habits.

Some workers have attempted to study the relation between longevity and food habits by analyzing the food preferences stated by octogenarians. Even though much valuable information applicable to immediate conditions may be secured by such verbal records, yet the validity of the data depends solely upon memory—a faculty which is subject to too great an influence from immediate experience to be trusted for an accurate record of the foods demanded at various stages of life at least half a century earlier. A study of the potentialities of the aged (Benedict and Root, 1934) requires information on the years that have preceded and on the mode of life which has made longevity possible.

satisfactory test rations. For example, the writer tried several years ago, in making a biological assay of a new vitamin D-carrying protein, to compound a ration which would not only support normal non-rachitic growth but would also prevent the occurrence of any new deficiencies which might result from a new combination of foods. In the face of the failure of methods based upon standard chemical formulae and mathematical calculations to produce a ration which would be completely adjusted to the delicate interaction of foods, he found that the nutritive instincts of the superior animals indicated to him a much more satisfactory balance (Dove, 1934, p. 230).

Uncertainty as to the interaction of foods also interferes in nutritional work with the determination of net energy values and the specific dynamic effects of balanced diets. Forbes (1933) has proposed as a goal in the determination of net energy values a ration based upon the "law of maximum, normal nutritive value," *i.e.*, "a ration which is qualitatively complete and quantitatively sufficient," since "an individual foodstuff expresses its normal and most characteristic nutritive value only as it is a part of a ration which is qualitatively complete and quantitatively sufficient. . . ." Forbes (1935) applies this concept of interaction to specific dynamic action when he states: "We are free to admit, however, that if—as we have concluded—net energy values of individual food stuffs are not constants, because of the supplementary effects of food combination, in rations, and other conditions affecting the economy of food utilization, then it is conceivable that, for similar reasons, specific dynamic effects of the individual nutrients likewise are not constants." Furthermore, Forbes (1935) specifies "heat increment" as the term which should be used to signify other dynamic effects—that is, "those which are not specific of particular kinds of nutriment."

Forbes, however, has not proposed a method whereby one may determine that ration which is "qualitatively complete and quantitatively sufficient." Neither has he

considered the possibility of an interaction between genotype and food. These experiments on the nutritive instincts had their inception to a large extent in an endeavor to find a means of determining those unknown complementary factors of foods, the detection of which at present lies beyond biochemical technique. A solution of this problem requires more than a consideration of nutrients and their combinations and interactions. The solution requires a recognition of genetic factors in the experimental animals—a recognition not only of the interaction between foods but also of the interaction between genotype and food. We have shown how the recognition of individuality in the nutritive instincts makes possible the determination of what is considered the optimum genetic potential activity, function or form, with the particular foods under consideration. Only by taking into account the genetic drives can all interactions be considered and a ration secured which is “qualitatively complete and quantitatively sufficient” for the optimum gene-nutrient combination of the particular strain of animals.

At the present time the rationing of all classes of live stock rests in part on *science* and in part on the ancient *art* of husbandry. Many of the present-day live stock rations are based upon the convenient old “five-bag-mixtures” with occasional modifications to include as additions widely varying amounts of those minerals and vitamins which the new nutrition deems important. When the same foods are given to animals for free selection, the *wisest* will choose very different ratios and combinations of foods—to suit the demands of his genotype and the interaction of foods—than have been selected for him by the nutritionist and, in so doing, is able when the correct assortment of food is before him to select a combination that makes him superior to the animals fed by the present scientific methods of rationing.

However, the method here proposed, to determine the proper mixtures of foods for live stock rations by recogni-

tion of instinctive demands, is not so simple as it may appear on the surface. There are many problems (as already presented)—in maturation, habit, social interactions, availability of foods, variations in nutritive value of foods, variations in genotype, degree of freedom, individuality, etc.—which must be analyzed before the nutritive instincts can be extensively applied to the formulation of rations for live stock feeding. But despite difficulties, this method recognizes both social and genetic interactions—two important nutritional influences which have not been considered heretofore by nutritionists—and supplies a means for a study of the interaction of foods whereby the best combination of those nutrients and elements available—neither too much nor too little in quantity, quality and balance—is supplied to the animal in accordance with its genotype.

AVAILABILITY OF FOODS AND THE NATURE OF THE FOODS
AVAILABLE AS FACTORS IN SURVIVAL AND IN THE
NATURE OF THE SURVIVING TYPE

Regardless of innate abilities or learning, each individual will be limited in its development by the nature and the variety of foods available. Individuals which by chance or misadventure are required to subsist on a limited variety of foods or upon foods in any way deficient are in as difficult a position as are the individuals who, though surrounded with all the varieties of superior foods required for an optimum existence, are unable to choose wisely.

The relation between availability of foods and growth is shown in Table XII, taken from a few of the preliminary experiments on chicks, which indicates the growth attained at three weeks of age by five different groups of chicks having access to five different assortments of foods.

The first two groups, A and B, were permitted access to only two different grain foods, oats and corn (1 per cent. cod liver oil in the corn), both grains known to be lacking in the essentials for normal growth.

TABLE XII

THE RELATION BETWEEN GROWTH AND THE KINDS OF FOOD AVAILABLE (WHEN FOODS ARE PRESENTED FOR FREE-CHOICE SELECTION)

Weight at 3 weeks of age (in grams)	With food assortment*				
	A	B	C	D	E
	n	n	n	n	n
Dead	12	29	2	7	1
30 grams	8	8			
40	10	27	1	3	1
50		18	2		2
60		13	5	6	4
70		4	7	17	2
80		1	9	24	2
90			11	11	4
100			15	26	5
110			14	13	7
120			8	21	7
130			13	12	7
140			8	24	8
150			5	17	11
160				14	15
170			3	8	7
180				7	13
190			2	1	4
200					3
210					3
220			1		
230					
Total number†	30	100	106	211	106
Average weight	35.5	47.3	108.7	115.9	140.5

* Food Assortment A = Yellow Attrition Corn Meal (1% Cod Liver Oil) and Oat Meal.

“ “ B = Yellow Attrition Corn Meal (1% Cod Liver Oil), Oat Meal, and Oyster Shell Flour.

“ “ C = Yellow Attrition Corn Meal, Fish Meal, Bone Meal, Oyster Shell Flour, Wheat Bran, *Alfalfa Leaf Meal*, Oat Meal.

“ “ D = Yellow Attrition Corn Meal, Fish Meal, Bone Meal, Oyster Shell Flour, Wheat Bran, *Wheat Middlings*, Oat Meal.

“ “ E = Yellow Attrition Corn Meal, Fish Meal, Bone Meal, Oyster Shell Flour, Wheat Bran, *Dried Skim Milk Powder*, Oat Meal.

† Based on Rhode Island Red chicks.

Group B had, in addition to corn and oats, an opportunity to select at will a readily available form of calcium (oyster shell flour). As a consequence, even though relatively small amounts of calcium were consumed, a much higher rate of growth to three weeks was attained by group B than by group A. Furthermore, the nervous and erratic behavior characteristic of the chicks in group A did not occur in those of group B.

Groups C, D and E received a fairly complete assortment of foods for free selection—at least sufficiently complete that the most wise could balance a ration for normal rate of growth. Mortality in these groups was reduced to nearly a minimum. The three groups received the same six foods, but in addition to these six similar foods, group C had access to alfalfa leaf meal, group D to wheat middlings and group E to dried skim milk. Group C did not do so well as the other two—the chicks disliked alfalfa. Wheat middlings (group D) brought about a distinct increase in growth, while dried skim milk (group E) produced the best results of the three.

These examples have been selected from a long series of similar tests made in this laboratory on the relative importance of the foods available and the effect of varying combinations of foods. They represent in a simple manner what has already been known—that some foods and some combinations are superior to others. But the experimental method is new in that it brings out the potential supplementary value of foods, a result which thus far has not been secured in nutrition experiments on mixtures of foods.

The two examples of Table XII not only illustrate the fact that calcium and milk have nutritional advantages. The relatively important part which lime and milk have played in the nutrition of both animal and man, especially during the period of early growth, and the contribution they have thereby made, throughout the history of civilization, to the nutritional welfare of the group are facts already widely recognized. The greater importance of

these experiments lies in the fact that, by making evident the great value of *accessibility* to lime and milk, they show that each food has palatability and value in accordance with its ability to contribute some nutritional factor not found in the foods already available.

The unavailability of essential foods and the nature of the foods which are made available lie at the root of the present-day problem of nutritional deficiency diseases in both man and live stock. For instance, there are still large sections of the country engrossed in the production of crops deficient in vitamin A (white corn, white potatoes, white-heart cabbage), although people and livestock in the same regions show signs of vitamin A deficiency. The unavailability of essential vitamins and minerals is manifest in many parts of the world, acutely in so-called misery spots but in a chronic and sub-clinical manner in practically all regions. The permanent prevention of deficiency diseases resulting from such conditions and the release of a people from a large part of their physical suffering and the cost of medical attention may be best brought about by a consideration of the nature of the nutritional environment and the varieties of foods and crops which should be grown in any delimited area (Dove, 1934, pp. 191-194, 264-274).²⁴

²⁴ In a recent report of experiments by the author, this anthropogeographical attitude is taken toward the vitamins and minerals supplied in one such delimited area, Maine.

The publication stresses the unavailability of calcium in the foods of the people and the live stock (a lack aggravated by a lack of vitamin D, ultra-violet rays and possibly phosphorus) and the deficiencies which have resulted from this unavailability. Permanent correction of such deficiencies, it is emphasized, must come through methods of increasing the opportunities for a choice of foods endowed naturally with essential adjuvants and of thereby forming proper food habits among the young inhabitants of the state.

The unavailability of calcium is also one of various causes contributing to the unavailability of vitamin A, inasmuch as acid soils do not support the growth of legumes rich in vitamin A, such as alfalfa. Dairy cattle fed non-leguminous forages, low in vitamin A, produce milk and butter only one tenth as valuable in vitamin A content as milk and butter from legume-fed animals. Vitamin A deficiencies in the people, mirrored in the high incidence of respiratory and other defects (Dove, 1934, p. 205),

are probably accentuated by a diet consisting largely of easily available white potatoes (instead of yellow potatoes, rich in vitamin A, or green vegetables).

Information concerning other deficiencies in vitamins and minerals has been secured by the writer in a study of the vitamin and food-mineral resources of Maine. An analysis of the physical examinations of men entering the University of Maine in 1933 reveals the fact that the individual incidence of carious teeth and of teeth missing is twice as frequent among Maine-reared men as among the men sent to the university from out of state.

OCURRENCE OF TEETH DEFECTS AS RELATED TO BIRTHPLACE AND RESIDENCE
(MEN STUDENTS ENTERING THE UNIVERSITY OF MAINE, FALL, 1933)

		Non-carious n	With carious teeth n	With carious teeth per cent.	Full mouth n	With teeth missing n	With teeth missing per cent.
Birth	{ in the state	174	18 = 10.34		101	50 = 49.50	
	{ out of the state ..	100	7 = 7.00		45	13 = 28.89	
Present home	{ in the state	212	21 = 9.91		127	65 = 51.18	
	{ out of the state ..	62	4 = 6.45		81	26 = 32.10	
Birth and present home	{ in the state	137	14 = 10.22		155	78 = 50.32	
	{ out of the state ..	54	3 = 5.56		53	13 = 24.52	

In order to prevent deficiencies in vitamins C and D and calcium, of which these teeth defects may be considered symptoms, varieties of the available fruits, vegetables and animal by-products must be selected whenever possible for these advitants. An excellent opportunity for increasing vitamin C availability, for instance, presents itself in varietal selection of apples (Maine's premier fruit crop). Those varieties, if adaptable, which are now known to be very potent sources of vitamin C (Northern Spy, Winesap, Ben Davis and Baldwin) should replace those varieties which are very poor sources of vitamin C (Jonathan, Delicious, Tolman and McIntosh). (See Fellers, Isham and Smith, 1932; Smith and Fellers, 1934.) In Maine the varieties of vitamin C-rich apples would add enough vitamin C to meet the yearly requirements of 200,000 more people (in 1930) and 440,000 more people (in 1920) than the vitamin-poor apples would supply. Again, since the common variety of the low-bush blueberry is also low in vitamin C as compared with other varieties not so common (Fellers and Isham, 1933), selection in this fruit, as well as in other fruits and vegetables, for the varieties containing the advitants deficient in the region should in time permanently reduce the frequency of vitamin C deficiencies among the people.

These suggested changes in varieties of fruits and vegetables grown or the development of new varieties of high-vitamin content must of necessity be made slowly; more than a decade is required to grow a new variety of

Factors which hinder and postpone the making available of foods known for a long time to be essential to health but not made universally accessible even to-day include:

(1) The persistence of food habits and food-processing methods passed on from parent to offspring as a form of transmitted inheritance.

(2) The difficulties surrounding attempts to reeducate these obstinate food habits.

(3) Geographic, climatic and soil fertility problems which lie behind the production of foods to be made available.

(4) Economic factors relating to food production based

apple. However, fortunately or unfortunately, the faulty food habits of a race also are exchanged for better food habits only in terms of decades. Attempts quickly to increase the availability of vitamin C through suggestions to the people that they increase the production and consumption of such annual crops as cabbage, tomatoes and spinach run into difficulties equal with those encountered in the selection of new varieties of apples. Suggestion alone can not readily cope with ingrained food habits and with the old-fashioned cooking methods known to destroy the heat-labile vitamin C. Thus there seems to be no quick and easy method for increasing accessibility to a correct assortment of foods. But in a state unable as it is to grow citrus fruit crops, the principal fruits and vegetables, especially those consumed raw and produced in large quantities, such as the apple, should be selected according to their vitamin content. In the interest of permanent prevention of nutritional deficiency diseases this proposed *vitamin (or mineral) sieve* should come first in importance in plans for variety selections.

If horticulturists and agronomists could specialize in their variety selections for fruits, vegetables and grains known to be high in the vitamins and minerals generally lacking or deficient in the foods available within the boundaries of their own market areas, they would in time, through the increased availability of these varieties and classes of food and through educational means be able to instill within the consumer a demand for such foods based upon an actual liking. After a taste for such foods has been developed and made relatively permanent through habit, the necessity for an appeal to reason for positive vitamin and mineral demand might well be discarded, since the increased availability would gradually foster, through habit, a natural demand for the advitants of survival value. Furthermore, such an abundance of and easy access to vitaminized foods would prevent the harmful psychological complex known as "food worries," induced in the present generation by the necessity for retraining in food habits.

upon the profit motive of commercial growers and producers of food.

(5) Nutritional and physiological response to social customs, and quasi-medical judgments.

All the factors which make inaccessible the foods essential for the development of a superior human race logically should be handled through a socialization of medicine. The problem is so immense that its solution must enlist the contributions of psychologist, anthropologist, geographer, nutritionist and physician. Judgments so important to human welfare should not be left to the isolated attack of any single science—certainly not that of “practical agriculture.”

SURVIVAL VALUE OF IMITATION AND ASSOCIATED SOCIAL
FACTORS IN THE CHOICE OF FOOD, AND ITS
RELATION TO EVOLUTION

All forms of life owe their existence to the ability of past generations to select from their nutrient environment, either individually or cooperatively, the food elements required for the maintenance of life. In those forms of life dependent upon sexual reproduction, this ability to select food must insure life up to the age of sexual maturity and reproduction. In non-motile and sessile forms of life, this ability to choose nourishment has persisted largely as a function of cell physiology through what may be termed differential absorption from elements in the immediate environment. In motile forms, especially among animals, the expression of the choosing process is facilitated by a roving nature, which makes more accessible to cellular absorption or adsorption those nutrients required by the organism. Even in some of the lowest forms of life, such as the amoeba and the protozoan (Schaeffer, 1920), this ability to select nourishment is well developed. However, its highest development is encountered in the higher organisms. Some birds, after the complete absorption of the body yolk into the blood stream, and practically all mammals, after the suckling

period, are thrown into an absolute dependence for survival upon their ability to choose wisely. Among domesticated animals, even though they may be fed so-called scientifically devised rations, there is still a dependence upon a certain amount of freedom of choice of foods, inasmuch as the all-mixed ration has not as yet been perfected.²⁵ The nutritive instincts are still ahead of the science of nutrition for many classes of animals and must still be relied upon in part for all animals.

The young of the human species, after weaning, gradually attains a range of freedom in choice of food wider than that found by the most omnivorous of animals.

²⁵ So-called "complete" rations, with all the foods mixed into one ration, have been made for some classes of live stock and for small laboratory animals. Many of these rations are dropped after a few trials, but others continue to produce excellent results over a period of animal-generations. These latter certainly must contain the essentials for growth and reproduction, and for longevity up to the time of sexual maturity. They are necessarily adapted, however, not to special activities or functions—except as quantitative adjustments may be made by the animal—but to the support of an *average* type of existence. For instance, the highly specialized dairy animal of to-day can not maintain high milk production on pasture alone, one of nature's "mixtures" for the support of unspecialized existence. When the same food is offered to the animal to support such diverse functions as growth, reproduction, milk secretion and the maintenance of long life, the maximum efficiency for any one function can not be expected.

The all-in-one ration may be questioned on still another ground, namely, that through natural selection many species of animals have evolved, under the necessity for a free choice of food, a variable diet. The monotony of an all-mixed ration may not be compatible with the present surviving type. Some species (notably insect pests) are confined by nature to a single diet, from which very little choice can be made. The nutrients required for different stages of life in such species must come through a differential absorption combined with a limited variation in functional activities within each stage of life, and through a complete change in diet for the pupal, larval and adult stages in the life cycle.

The ability of an organism to develop specialized functions—one sign of evolution—requires an ability to choose food for that specialized function. Birds laying daily will choose to consume several times as much calcium-bearing food as will the intermittent layer. Thus we should find higher variability in food preferences associated with evolutionary trend toward superiority in specialization. The primates are more variable in their food preferences than rats, pigeons and hens (Maslow, 1933) and man appears to exceed all animals in the variety of his appetite (Katz, 1930).

Man's survival and the nature of the surviving type rest to a large extent upon his ability to choose food wisely, both in quantity and in quality.

In both lower animals and man, dependent as they are upon a wise choice of food for survival, we observe another factor entering into their activity which modifies considerably the choice of food, the quantity of food consumed and consequently the survival value—and that is the effect of suggestion and imitation. Observations by the writer on the feeding habits of the young of horses, cattle, swine, goats, rabbits, chicks and other domesticated animals indicate that the young learn very early to follow and imitate the mother in the time of feeding and in the foods consumed. A common instance of suggestion on the part of the mother is that of the broody hen who "calls" her chicks to come to the food which she herself has chosen for them. When a number of chicks are placed together in a single compartment we notice the strong influence of suggestion and the resulting imitation in such behavior patterns as the quick response of newly hatched chicks to a moving object or to sound. Reactions toward movement may be observed in the flocking and the drinking reactions. When one chick darts off toward the opposite side of the compartment, those nearby fall in with him. In this manner the chicks tend to "flow" in groups which increase and diminish with the activity of a leader and with the amount of dispersal in group movements similar to those of swimming schools of fish or of migrating birds. Reaction toward movement also may be observed in the response of day-old chicks to the sight of a head thrown up in the drinking and swallowing reaction. The sight of a chick's drinking water immediately attracts the observers, who even though they may never before have done so do likewise. Reaction to sound may be observed in the sudden rush of chicks toward the chirping of those who have found food. Thus it is noted that within a group of chicks the contact with food and drink is facilitated by the social interactions of the group as a whole.

That such social interactions as those we are discussing actually affect the structure and function of the organism and thereby become biologically important is a conclusion to which these experiments on growth constantly point. That is, the final form and function of the organism is dependent not alone upon hereditary and environmental (nutritional) factors and their interactions, but also upon those social factors expressed as the interaction between individuals. Let us take, for example, the phenomenon of growth. *Hereditary* factors (expressed in part through a selection of food in both quantity and quality and through a selective absorption and efficient utilization of nutrients) contribute the genetic drive. *Environmental* factors related to nutrients, which may even accentuate or modify the hereditary drives, supply the building materials. But the *social* interactions intimately related to feeding—such as imitation, suggestion, leadership, dominance-submission, social facilitation (greed)—also affect this phenomenon. No longer can the geneticist and the nutritionist consider such a problem as that of growth their property, so greatly do the social interactions modify the effects of heredity and environment. These social influences, transmitted as they are from generation to generation through habit, come to form as powerful an element in moulding the form and function of a race as would a defective or superior gene, or a permanently deficient or fertile soil or food.

We come, then, to the most pronounced of the social interactions observed in these experiments. Within each group we must consider two kinds of individuals—the leaders and the followers. The leaders are the first to dash for food or drink, the followers ever fall in behind. During early life when the young are under parental care the parent takes the place of leader, in some instances, as in the wild bird nestling period, assuming despotic control over food choice. When the young animal is freed from parental control, there is substituted a social control expressed in group feeding reactions. Imitation comes to

be supplemented or supplanted by such reactions as "Fütterneid" (greed for food) (Bayer, 1929; Ziegler, 1920), recently termed *social facilitation* by Harlow (1932), and also by ascendance-submission (Harlow and Yudin, 1933). That such strictly social factors as these come to be strong influences upon the nutritional life of each individual will be shown immediately.

In an analysis of group feeding reactions the end-result (growth rate) would seem to indicate that the leader to some extent guides the food choice of the group as a whole, and that the final effect of this leadership is similar to the effect of parental food habits upon those of the offspring. At least we may say that the end-results of "greed" for food and of imitation are, in some respects, the same. In both instances food choice and the quantity of food consumed are partly controlled by the leader or by the parent. The complementary action between parent and offspring and between leader and follower has even more subtle similarities. In both instances the mother or the leader suggests the food to be consumed and the amount of time to be spent in eating, while the offspring or the follower may imitate or greedily follow. Both parent and leader may sacrifice their own interests and even life for the imitators. The mother hen will fail to consume food herself and will become thin while she finds food for her offspring. The cockerel will also fail to consume enough food when overly anxious about the search for food for his females. (We recall the political and religious leaders who practice self-sacrifice or even sacrifice life itself in a similar manner for their followers.) Both imitation and social facilitation (greed) have immediate as well as racial survival value. Imitation is the inherited form of social facilitation and is therefore more complex. Imitation stands to social facilitation as instinctive response stands to reflexes: Both imitation and instinctive response are racial traits, while social facilitation and reflexes are the superficial, simple, individual expressions. Thus, though social facilitation

(greed) may appear more selfish than imitation, both are self-concerned with regard to racial and individual survival.

Leadership control over the choice of food made by a group may be recognized by the ratios of foods consumed by each group permitted free access to similar foods. For instance, when a number of different groups of chicks are permitted to choose from a similar variety of foods and the groups are left intact so that a social order is built up for the growing period, we observe that the ratios of foods consumed by each group vary widely, as do the ratios secured from single isolated individuals. The wide differences between groups, furthermore, remain relatively constant throughout the growth period. The effect of leadership will be most definitely expressed as a variance in the rate of consumption of the food in highest demand, since in such a case the leader would have a relatively large number of times in which to exercise his leadership.²⁶ This effect is clearly shown in the percentage of corn—the favorite food—consumed by ten different groups for four different periods of growth, as listed in Table XIII.

According to this table, 6 out of the 10 groups are consistent in consuming in every period an amount of corn meal above the average (or below the average), while 2 of the remaining 4 are consistent for three fourths of the growing period.

That leadership to the feed (in the foregoing case, corn) is responsible for the consistent preference for the food receives corroboration from visual observations on feeding behavior. The first chick to start feeding (the leader) generally attracts others and in a short interval all ten chicks are eating from the same food pan. At such times

²⁶ The power of a single leader will be found, it is thought, to affect only small groups, since the members of large groups tend to vacillate more freely from one leader to a number of leaders or sub-leaders—an important leveling factor. In the experiments where the continuous domination of the same leader was not desired, a bi-weekly regrouping of all the members was practiced.

TABLE XIII
EFFECT OF LEADERSHIP UPON GROUP CHOICE OF FOOD*
(Percentages of Corn Consumption)

Group	Age			
	3 to 5 weeks	5 to 7 weeks	7 to 9 weeks	9 to 11 weeks
431	49.92%	62.11%	64.38%	71.58%
432	58.60	56.20	66.45	57.99
433	54.35 -	54.24 -	61.16 -	62.59 -
434	63.32 +	60.81 +	71.28 +	70.07 +
435	55.01	60.41	59.52	69.15
436	55.75 -	52.77 -	65.98 -	59.12 -
437	63.19 +	65.79 +	70.26 +	74.73 +
438	48.24	60.54	69.02	69.27
439	59.59 +	62.74 +	69.04 +	72.34 +
440	60.23 +	67.73 +	70.69 +	73.09 +
Ave.	56.82	60.33	66.78	67.99

* Records based on 100 Rhode Island Red chicks (at start of experiment).

the desire for the food consumed by a neighbor is so great that the individuals at the ends of the feeder will attempt to crowd into the midst of the group, even though adequate free feeding space is available at the edge.²⁷

The power of the leader to suggest food is apparently followed only to the feeder—and does not or perhaps rarely, if at all, carry over into a selection of foods out of a mixture. When in a mixture certain foods retain an identification mark, as of color or size, some individuals learn to choose and pick out a favorite type of food, but

²⁷ E. Bayer (1929) has shown experimentally that competition for food increases food consumption by hens. Even satiated birds could be induced by competition to consume 34 per cent. more food. Political leaders resort to social facilitation or greed for party interests. Note the obviousness of "Share the Wealth" and "Every Man a King" slogans by which both leader and follower wish to profit. Another striking example of imitation and social facilitation may be recognized in the reaction of scientists to a new lead. If the new lead is not too far from immediate experience, a feverish activity ensues as a circular response that spreads even into associated fields. The exploitation of an idea by scientific activity is essential to scientific analysis, since through the stimulation of competition a more thorough or accurate analysis is thereby projected. This activity tends to build up cycles of interest. Note the recent rise in interest in the cytology of giant chromosomes and the physics of heavy water.

the followers will not necessarily imitate the selection. The favorite food may have growth-promoting value, and the lucky chooser will consequently succeed in growing far beyond his associates who either dislike the particular food or have not discovered it. For instance, when dried egg yolk was mixed as small granules into a rickets-producing ration, certain individuals learned to pick out the deep yellow vitamin D-containing morsels and as a result grew to a size twice as large as other individuals in the same group with the same opportunity. As an example of this phenomenon, one individual grew to a weight of 775 grams in 11 weeks' time, while his next largest brother grew to only 560 grams.

These facts concerning the effect of leadership on the choice of food are very important from the evolutionary point of view, inasmuch as dependence upon the leader is reflected in the survival or non-survival of the group, or at least in variations in form and function which in themselves have survival value. The welfare of the group, in other words, depends upon the leader's ability. Only those groups which have leaders who are wise in their choice of food can form the material for future generations.²⁸

That leadership is an important factor in the nature of the surviving type may be recognized in the human species. Maternal desires for food are implanted into children. Peculiar acquired racial diets mould the final development of the individual, so much so that after a number of generations heredity for form and function can scarcely be separated from the effect of food on form and function. On the other hand, the changes in size of immigrants indicate that a new physical and social environment has modified older racial diets and has furnished a different quantity of those advitants which affect body

²⁸ Tarde in his "*Laws of Imitation*" (1890) recognized the fundamental identity of generation and imitation as a social phenomenon but failed to recognize the biological significance of the identity. Thus he regarded individuality as a fleeting essence, which exists only once and only for a moment (Davis, 1909).

size.²⁹ Such changes in body form may also be recognized in imported animals who may run to mediocrity if they are shipped into a region in which the soil, crops and environment are deficient in vital elements. Thus in the same way that the leadership of the mother in food choice affects the family type, so do the food fads of the group and the foods actually available to the group affect the racial type.

In connection with the relation of choice of food to evolution, we point to the fact that analysis in terms of leader-follower interactions may serve to clarify a difficulty which has constituted a frequent stumbling-block for the geneticist, namely, the failure of certain supposedly inherited characters to conform to the Mendelian scheme. A case in point is the observation of Castle (1929, 1934) that the offspring of reciprocal crosses between large and small races of animals are not always alike in size as would be expected on a gene factorial basis. Castle has shown that the offspring of small female rabbits crossed with large male rabbits, and of the reciprocal cross, tend to be in each case more like their mothers than like their fathers (1934). In view of this discrepancy from a genetic interpretation Castle concludes (1934, p. 624):

"that something besides chromosomal genes is concerned in the determination of body size in crosses between races of unlike size. Conceivably it may be genetic or non-genetic. If genetic, the egg cytoplasm would seem to be the most likely agency, as suggested in my 1933 paper. If non-genetic, some agency supplied by the mother during gestation might be held responsible for the observed difference. A decision between these alternative explanations can not be made at present, but must await further experimental study of the case."

Is it not also possible, in the light of the conditions explained previously in regard to maternal control over

²⁹ The Italian immigrant accustomed to goat's milk in his own country may fail to secure the needed calcium in this country through a dislike for cow's milk.

the food consumed by the young, that both small and large mothers tended not only to pick out of the slight choice of grain versus green food or forage the factors for growth but also to consume different quantities of food—and that this choice of foods (a qualitative result) and duration of feeding (a quantitative result) were imitated by the young (at least to the extent that the mother had relatively more influence than the father upon growth)?

Unfortunately we can not decide from Castle's report how the young were reared. The statement that "the majority were nursed by foster mothers" does not help toward a solution of the difficulty, since the foster mothers might well have been of the same size as the natural mothers. Furthermore, growth between the two crosses differed by an average of only 5 per cent., and even though this difference was statistically significant nevertheless it represents only a fraction of the difference in growth that may be brought about by alteration of food ratios. In the experiments reported in this paper, the group of chicks growing at the slowest rate gained only 372.0 grams from 3 to 11 weeks of age, while the group growing at the fastest rate gained 974.8 grams. The difference in gain is of a magnitude similar to the differences in weight of the smallest and the largest breed of rabbits used by Castle, *i.e.*, 1,500 grams for the smallest (A strain) and 3,500 to 4,000 grams for the large New Zealand white race. In both cases, in our chicks and in Castle's rabbits, the largest were approximately 2.6 times larger than the smallest group or race.

When the food selected by the two extreme groups of chicks, the fastest-growing and the slowest-growing, was fed to unselected but genetically uniform test chicks, the food mixture indicated by the fastest-growing birds produced larger birds than the food selected by the slowest group. To be exact, the food selected by fast-growing birds produced 23.7 per cent. larger growth than did the food selected by slow-growing birds. If the food selected

by individuals which grow at a fast rate can produce over 23 per cent. larger growth in an unselected test group, could we not expect the offspring of large, fast-growing rabbits to imitate maternal food habits to an extent that 3 to 7 per cent. greater growth would ensue—the extent of maternal influence noted by Castle in favor of the hybrid offspring of large mothers?

Other than social factors might help to produce the same result. For instance, the food selected by the mother during gestation not only might stimulate differential growth rate but also might produce in the offspring a desire for certain foods—two possibilities now being subjected to experimentation.

The mother's choice of food, then, can be considered a factor in the modification of those characters, especially growth, which seem to be outside the sphere of gene interpretation.³⁰ Since familial influences on food may definitely modify and even dominate inheritable characteristics, they constitute a factor which may assist organic evolution in modifying the race.

In short, then, familial and racial habits for certain varieties of foods may play as directly upon evolution as does sexual selection. Here in the case of food choice we have shown that food ratios selected by fast-growing individuals can increase growth rate in a significant manner. If form and function are so closely related to food choice and if we grant that at least some social interaction takes place to influence followers to consume the same foods in the same quantities selected by the leaders, we should expect to find the possibilities for directive change. We should expect to observe after a number of generations a gradual shift of the line toward the leader type and mutations toward new higher forms of

³⁰ Could not these factors of similarity in food consumption by long-lived married couples be responsible for the unexplained similarity between males and females in length of life encountered by Pearl and Pearl (1934, p. 58), and should not these same factors of similarity in nutrition be considered in studies on homogamy, in so far as nutrition may alter the organism after sexual maturity?

functional potentialities (provided that the nutrients for more extreme requirements are available). In this process we must recognize that social factors, extraneous to genes as they are, are nevertheless artifacts that glow as if endowed with genetic integrity of their own.

THE UTILIZATION OF THE NUTRITIVE INSTINCTS TO
TRANSCEND THE ACTUAL AND PRODUCE THE SUPER

The formulation of equations through the serial data secured on varying rates of a function (growth, for instance) makes possible the extension of ratios of foods in both the positive and the negative direction on and beyond the figures actually secured. By extending the regression line through each food percentage one is able to calculate the mixture required for zero gain in weight or even the theoretical ration required for loss in weight (assuming a linear regression in such extensions). On the other hand, by extending the straight line on and beyond the maximum rate of growth, it is possible to calculate the ration required for such rapid rates as have never been observed to take place.

The foregoing method of producing the super individual, if tested in its purest form, would probably prove impracticable because of genetic and physiological limitations, but the principle is mildly applied in the following experiment. Although very few individuals are able to remain in group 10 (highest rate of growth) during all four two-week periods, and although when an individual grows at a very fast rate for one or two periods he is very likely to drop slightly below the fastest-growing group during the third or fourth two-week period, nevertheless if the food selected by the top group of each period were to be fed to certain individuals throughout the four periods, such a method of feeding, quantitative adjustments notwithstanding, might be expected to force a rate of growth never heretofore observed. By using the actual ratios of foods consumed by the fastest-growing group each two-week period, we should be supplying food which

would usually bring out the optimum growth in the most superior individual. Since the optimum growth rate for the average was calculated as equal to the rate of growth represented by a value 71.1 per cent. of the standard deviation above the mean rate of growth, then a ration calculated for the fastest-growing individual would be excessive for some individuals but would furnish the exceptionally superior individual with the nutrients required for a growth which under any other conditions of feeding would seldom, if ever, be found and therefore seldom expressed.

In this way (not, however, from the food mixture selected by the chicks growing at the fastest rate but from one selected by those growing at a rate near the highest, *i.e.*, in the third group from the highest), the writer has been able to secure the largest group of individuals ever recorded in the laboratory under any other method of feeding. These individuals weighed at 11 weeks of age a value far above the average for the same strain of bird. The males averaged 1,464 grams and the females 1,155 grams in weight. The possibility, then, exists that through such a series of individuals ranked in degrees of ability—an ability depending upon definite food ratios—one might transcend nature's best method of rationing and produce the beast or the man superior in those qualities which are highly affected by the nature of the food ingested.

INDIVIDUALITY AND CONATION

The extensive problems related to the nutritive instincts, to which so little attention has been given heretofore, are certainly more extensive than can be elucidated in this brief résumé. Indeed the biochemical work necessary for complete elucidation must be preceded by much preliminary investigation.

Such investigation will seek, first, to eliminate or understand the causes of fluctuations due to psychological factors and, second, to find the exact mathematical associa-

tion between the genetic and nutritional factors which together govern the same function. It appears to the writer that the key to any investigation of the problem lies in a full and complete recognition and understanding of individuality.

The control of a natural process which an understanding of individuality makes possible for the nutritive instincts could, it seems to the writer, be extended to all processes that are conditionable. For example, educators could profit well by considering an individualization of their methods. Although they have claimed to consider the individual the center of pedagogic attention, they have not yet thought of establishing a system of serial rank according to proficiency so as to discover for the educator how to condition followers to the same proficiency indicated by the leaders.³¹

To the criticism that individuality has already been well recognized; that it is represented by the suggestion of Davis that children be permitted free choice of food, by such systems of education as the Montessorian, by individualistic psychologies which have been built up about the individual, by the recognition of the individual in political democracies and the dictatorship, by the hero worship of Carlyle and the Zarathustrian doctrine of the Superman—we make this answer: In all these attempts to evaluate *the individual* there is a failure to employ the

³¹ The nutritive instincts are seen to have an even more direct bearing upon educational methods when we recognize that certain food factors, other than energy, act as spurs to intellectual effort (Maurer and Tsai, 1929, 1930, 1931; Fritz, 1932; Bernhardt, 1934).

The effects of food upon various social factors are important phases of the problem. For example, food strongly influences the nervous and emotional state of the individual. It can be shown experimentally that access to one set of foods, *i.e.*, corn and oats alone, will produce individuals so nervous that they run themselves thin and become excessively excitable and irritable, but that when the same two foods are given with a third, the mineral calcium, the excitability is greatly reduced and life is prolonged (Table VI). By slight changes in the types of food supplied to an individual it is possible to induce fighting on the one hand or peacefulness on the other. Even cannibalism may be produced at will by methods of feeding. Thus the whole physical, mental and social status of the individual is closely associated with the choice of food.

ultimate principle of individuality. Such instances as those just cited represent mere isms—in which *the individual as such* is set up as a sort of *ding an sich*. Any such ism is doomed to sterility because of a failure to recognize the inevitable social link between individuals. The projectors of these isms have not recognized that any principle applied to the individual must be synthesized from the group and that only then does individuality constitute the element from which deductions and reapplications can be made. If all conative processes were subjected to this inductive-deductive approach, explained here experimentally by means of analysis of the nutritive instincts, there would be made possible a pragmatic approach toward a human utilization of that cosmic principle which for Schopenhauer was an abstract *Universal Willie* detached from the possibility of human exploitation.

CONCLUSIONS

This paper is a first report on a study of the genetics and physiology of the nutritive instincts and associated phenomena, based upon a number of years of laboratory experiments in which the rat, the chick and the dairy calf were used as experimental subjects.

On the basis of these experiments and inferences derived therefrom, the following working principles or laws of the nutritive instincts are here proposed:

I. The nutritive instincts, manifest in a choice of food, are measurable and distinctive characteristics of the individual with a consistency that indicates the existence of biological principles guiding their expression.

II. The expressions of the nutritive instincts *vary* from individual to individual—some individuals appear wise and others unwise (less wise) in their choice of food.

This fact contraindicates against the *group* technique of free-choice feeding recently recommended for both animals and children.

Choice of food is not entirely the result of experience and habit. In fact, the nutritive instincts are principally innate, "purposive" or directive reactions expressed

with varying degrees of accuracy from the first contact with food and altered with the altered demands of the organism.

III. Variations in the nutritive instincts from individual to individual are due principally to innate differences. These innate differences may be accentuated or modified by imitation, limitation of opportunity and social adjustment, and may be stabilized by habit.

IV. Regardless of the origin or cause of individuality in expression of the nutritive instincts, the choice of nutrients varies in direct mathematical relation with the demands for bodily development and functional activity. This covariability between choice of nutrients and form or function may be expressed equationally, and when so expressed and reapplied to the feeding of groups of individuals genetically similar, may be used to modify that form or function within the limits of the phenotype.

Such an equational expression of choice of nutrients and genetic response may be used:

A. To determine the optimum nutritive requirements, both qualitative and quantitative, for a particular genotype—a mathematical expression of the interrelation between heredity and environment.

B. To determine the minimum and the maximum potential expression of the character resulting from the interaction of the specified genes with certain specified nutrients.

C. To constitute a technique:

(1) For the detection of causes of nutritional deficiency diseases, and the nutritional factors which contribute to longevity and other desired characteristics of the organism;

(2) For the biological assay of complex food substances;

(3) For the analysis of the complementary action of foods; and

(4) For the rationing of animals and men of different genotypes.

D. To discover the combination of nutrients best

adapted to each new genotypic complex as it is modified through genetic selection or as it shifts naturally in the process of evolution.

E. Either to restrict or to stimulate development or function, and, as a consequence,

F. To transcend all known existing values in the controlled production of the infrabeast and the inframan as well as in the realization of the superbeast and the superman.

V. The foregoing laws may be applied as a cosmic principle to all phenomena in which both a controllable individuality and a conditionability exist—not alone to those biological activities classed as instincts, reflexes, drives and wishes, but also to the higher faculties as of the intelligence, to the will, to group factors (social, educational and religious) and to all conative processes—and through their application the optimum genetic potentialities of the individual may be realized, even the character of the genetically superior may be stamped in part upon the inferior, and the superior itself may be transcended.

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